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Ecological Impacts of Forest Disturbance on Ring-Tailed Lemurs (Lemur Catta) in the Beza-Mahafaly Special Reserve Region: Implications for Conservation in an Altered Landscape

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ECOLOGICAL IMPACTS OF FOREST DISTURBANCE ON RING-TAILED LEMURS (*LEMUR CATTA*) IN THE BEZA-MAHAFALY SPECIAL RESERVE REGION: IMPLICATIONS FOR CONSERVATION IN AN ALTERED LANDSCAPE.

by

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Ecological Impacts of Forest Disturbance on Ring-tailed Lemurs (*Lemur catta*) in the Beza-Mahafaly Special Reserve Region: Implications for Conservation in an Altered Landscape.

Thesis directed by Associate Professor Michelle L. Sauther

Forest disturbance, both natural and anthropogenic, has been recognized as a severe threat to primate populations on a global scale. Moreover, primates tend to vary, between species and between sites, in their tolerance and response to disturbances. Perhaps because of this variability, the effects of ecological perturbations on primates remain relatively poorly understood. Understanding disturbance effects and the ecological variables that are particularly potent for primates will provide sound data for effective conservation management. In this dissertation, I examine the effects of anthropogenic disturbance and a destructive cyclone on the ecology and behavior of the ring-tailed lemur (*Lemur catta*) at Beza Mahafaly Special Reserve in southwestern Madagascar. I present data from four study groups (two in the protected Reserve and two in anthropogenically disturbed, unprotected habitats). Cyclone Ernest affected this region when it made landfall in January of 2005, seven months prior to the beginning of this study. These natural and anthropogenic disturbances have altered forest structure and phenology. Groups inside the Reserve tend to eat more terrestrial herbs and vine leaves. Additionally, Reserve Groups also rely on a fewer number of species for the majority of their diet. It appears that in more marginal habitats, *L. catta* is able to diversify its diet and exploit foods that might not be their primary choice. Non-Reserve Groups also inhabited smaller home ranges, but had higher daily path lengths than groups residing in the Reserve. Additionally, Non-Reserve Groups utilize open canopy areas and habitats with higher degrees of disturbance to a

greater extent than Reserve Groups. Non-Reserve Groups spend more of their active time both feeding and traveling than groups inside the Reserve. Non-Reserve Groups devoted less of their time to resting compared to Reserve Groups. Groups in unprotected habitats have greatly reduced group cohesion, lower rates of grooming, and elevated levels of aggression. Preliminary data show higher rates of injury and mortality for groups living outside of the protected forest. Anthropogenic habitat alterations, coupled with stochastic changes from tropical storms, have changed the landscape both in and around BMSR and contributed to survival challenges for *L. catta* in the area.

This dissertation is dedicated to Jason and Aidan –
for living this project with me and finding the strength to help me through it.
And for Aamion, who will also know the wonder of Madagascar and its lemurs.

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I have been lucky, fortunate, and sometimes undeserving to have the biological anthropology faculty team at the University of Colorado at Boulder supporting, teaching, guiding, and prodding me along. To thank them appropriately, I need to step back a few moments in time to my first introduction to anthropology. I was 18 and working for a few weeks at a refugee camp in Thailand. I met a woman who was doing interviews, and focusing on mother/infant care in the camp. I was enthralled – who was this woman and what kind of job lets you embed yourself in a culture, learn the language, and then apply your work to help people? Her answer was simple, "I'm an anthropologist." Enough said. That fall, I took my first anthropology class and was hooked. I was drawn to anthropology's holistic look at biology, humanity, culture, and evolution. My path to focusing on primates was circuitous. Starting with my first field job living in a monastery with Buddhist monks in Indonesia, to digging up hominid fossils near Lake Turkana, I found myself shying away from directly engaging with people and needing something more dynamic than a toothbrush scraping away dirt on a fossil. One day, as I was pulling out my fiftieth ostrich eggshell bead of the day next to Lake Turkana, a troop of baboons sauntered past. That's the ticket, I thought – extant primates. This circuitous route has been my foundation to truly appreciating anthropology's multifaceted, multivariable approach to examining the natural world, and the interplay between humans and earth's natural history. My faculty support at CU has built on this foundation because they are all true anthropologists and scholars– while they are laser focused on the intricacies of their own research, they also fundamentally understand, and speak eloquently to, the larger picture, the holistic perspective and anthropological paradigm that is essential to true anthropology. Culture, biology, evolution, history, are all part of their anti-myopic views of the world. This perspective is invaluable to the

students they reach every day in lecture, their graduate students, and the world they reach through their research. My committee, Dr. Covert, Dr. Dufour, Dr. Sponheimer, and my advisor, Dr. Sauther, are each true anthropologists, and I am indebted to them for instilling this quality in my own anthropological perspective and being able to apply it beyond the academic world. Dr. Armstrong, an exceptional teacher and source of knowledge, was instrumental in my training to placing primates within the wider context of mammals and the natural world, and asking the very important question, "why is a mammal?". Thank you for working with me over my graduate career and participating in my committee.

Dr. Michelle Sauther first introduced me to Madagascar and its lemurs. I remember standing next to her as dusk approached and looking up at a troop of brown lemurs scurrying through the canopy covering the red road we were traveling on. Our next sighting was a group of sifakas vertically clinging and leaping along the Mangoky river – I was hooked. I am indebted to Michelle for spending the time to coax the scientist in me along, sculpt my ideas into hypotheses, and guide me in crafting my project. She is a gifted scientist, teacher, mentor, and friend. I hope to take her perspective and channel it into my own niche. I'm not sure either of us knew how much of life happens while we are in graduate school, or how much the advisor is critical to the momentum of motivation: She flawlessly rose to the occasion and has never doubted my ability to achieve my goals. I have always been able to rely on her for support, friendship, sound judgement, and inspiration – even from far away. I admire her dedication to BMSR and firmly believe that sound conservation comes from passionate individuals who invest years in understanding the dynamics of their forests; The ring-tailed lemurs at Beza are lucky to have Michelle.

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During my fieldwork, several important people helped me with my research, and contributed to making daily life easier and full of tremendous memories. Hallie Jensen (now St. Onge) came on this wonderful adventure with my family and me and rose to the occasion every day helping me run after our 2-year old, collect data, search for hard to find lemurs, and is a great friend. James Loudon - fellow graduate student, primatologist, and all around great guy – helped

make a very long year in the field tremendously rich with laughter, conversation, music, and friendship. James is a true friend, and I am lucky to count him as one of mine.

Several people helped make the writing process move forward as a I took a position at a natural and cultural history museum before I had finished writing, and I thank them for their patience and motivation. Paul Thoma spent countless hours with me and my statistics - always with a helpful spirit and timely responses: Thank you for repeatedly explaining the same concepts. Janeanne Upp believed in me, motivated me, and has given me tremendous opportunities to apply anthropology in the museum world: thank you.

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While he won't remember every detail, my son Aidan was an integral part of this project, and I will always remember sharing fieldwork with him. He was two years old when we arrived in Madagascar and he spent the year making up his own Malagasy/English dialogue with Tsamsia, playing in dirt, eating mangos, spotting the lemurs when I couldn't, and keeping Jason and me on our toes as we potty trained and kept him safe from scorpions. Seeing Madagascar through his eyes was priceless.

I am saving the most important thank you for last. Jason, my husband, traveled and worked side by side with me, kept our son safe and having fun, and supported my dream of living with primates. I hope I can return this gift to him someday. My thanks can never be enough.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

ANTHROPOGENIC HABITAT DISTURBANCE AND ITS EFFECTS ON PRIMATES

1.1 Ecological effects of Anthropogenic habitat disturbance

Anthropogenic habitat disturbance is considered a chief threat to species worldwide (Cuarón 2000, Erlich 1988, 1995, Groombridge 1992, Law and Dickman 1998, McIntyre and Barrett 1992, Saunders et al. 1991). Habitat disturbance, referring to habitat loss and modification, is a broad concept that can occur as a stochastic event, or a gradual process. Currently, the dominant types of habitat loss and modification are directly related to human activities (Bender et al. 1998, Cuarón 2000, Travis 2003).

The ecological effects of anthropogenic habitat disturbance occur in several ways and affect communities on several levels. Most obvious are the ultimate effects of habitat disturbance: landscape change and declining numbers of species. These effects include the spatial configuration of the remaining forest. Several broad scale research approaches scratch the surface of quantifying the disturbance consequences. Indeed, images of devastated forests due to logging and clearing are painfully prevalent in the media. Typically, researchers can easily assess the area lost in the post disturbance landscape via remotely sensed imagery (e.g. Green and Sussman 1990, Skole and Tucker 1993). Furthermore, using species-area relationships, mathematically inclined landscape researchers can model the effects of habitat disturbance and loss on species by calculating the area lost (Connor and McCoy 1979, Cowlishaw 1999). Moreover, collecting simple census data provides a description of how many individuals are present from year to year (Boinski 1994, Muoria et al 2003, Yongzu et al. 1989). What is more elusive, however, and remains largely unknown, are the proximate mechanisms

(those mechanisms that directly affect animals in their day to day activities) through which anthropogenic habitat disturbance leads to population decline and eventual extinction. Broad scale approaches fail to detail the more subtle ways that habitat disturbance affects species. They fall short in documenting effects of the three major consequences of disturbance: proximate anthropogenic effects, degraded habitat variables that are the indirect effects of anthropogenic change, and the effects of landscape-level changes. These consequences affect flora and fauna on the proximate level; posing daily challenges for wildlife. In addition, these themes are particularly poignant in the field of primate conservation in light of the conservation crisis for our order's species (Chapman and Peres 2001, Cowlishaw and Dunbar 2000, Marsh 2003, Sechrest 2002). This dissertation will address the proximate effects of habitat disturbance on wild ring-tailed lemurs in southwestern Madagascar.

For animals living in anthropogenically altered habitats, there are several challenges that can be broadly grouped in the three categories mentioned above: proximate anthropogenic effects, degraded habitat variables and unsuitability of habitat, and the effects of landscape level changes.

1.1.1 Proximate Anthropogenic Effects

Humans can affect wildlife in a variety of ways both direct and indirect. Most potently and dramatically, however, are the direct effects of hunting, disease, and introduced predators on endemic populations. These are proximate factors that act quickly to decimate individuals and may drastically reduce population size. The following sections detail how human contact via hunting, introducing disease, and introducing predators can alter a population.

1.1.1a *Hunting*

In anthropogenically altered habitats, one of the primary proximate human activities that directly disturbs species in their natural habitat is hunting. Hunting as an ecological disturbance has been occurring for millennia in areas of the world and bushmeat has long been a part of the staple diet of forest dwelling peoples (Fa et al. 2000). What began as an ecological disturbance in balance with the environment has grown to an unsustainable practice in many areas. In fact, overhunting of wildlife is considered a primary reason for biodiversity loss in many tropical forest regions (Fa et al. 2002). It has been argued that it is not habitat loss, but defaunation that poses the greatest immediate threat to animal conservation in the forests of West and Central Africa (Wilkie et al. 1998). In an examination of a bushmeat market on Bioko Island researchers found 14,677 carcasses in 1996, compared to a field study in 1991 when they found 8,528 carcasses – a statistically significant increase (Fa et al. 2000). The number of identified species also jumped from 14 in 1991, to 21 in 1996. The authors also noted that while the number of carcasses has increased, the biomass has decreased from 1991 to 1996. To investigate the reasons behind this, they performed population censuses for these larger bodied species and found that the seven diurnal primate species and duikers have become more scarce. Despite the fact that the people of Bioko have ready access to an abundant source of fish protein, bushmeat is preferred over any other source of animal protein (Fa et al. 2000, Njiforti 1996). Other papers reporting bushmeat harvest data from this market location have argued that the 1991 market harvests already exceed sustainable levels for most primates and for the largest duiker species in this area (Fa 2000; Fa et al. 1995). Researchers also report that the data they present underestimate the situation by as much as 40% due to the numbers of animals that are hunted in villages, animals bought on the way to the market, and animals that escape with injuries,

decompose in traps, or become food for scavengers that their market data do not encompass (Fa et al. 2000). These data emphasize that while hunting wildlife is a central part of these peoples' diets, it has soared to unsustainable levels and wildlife populations, especially larger bodied species, are declining.

With a consistently growing body of literature documenting the bushmeat phenomena in tropical forests (Bowen-Jones and Prendry 1999, Robinson and Bennett 2000, Wilkie and Carpenter 1999), the general conclusion is that harvested populations show consistent declines in density, species being locally extirpated and wildlife populations being reduced to densities where they have ceased to be a significant resource for humans (Robinson and Bodmer 1999). The syndrome of the 'empty forest' (Redford 1992) has been discussed for more than a decade, and is most advanced in west and central Africa (Oates 1999). One study has compiled published data of hunter-kill profiles of mammals from 36 sites in seven countries in west and central Africa (Fa et al. 2005). These authors concluded that ungulates constituted about 73% of all hunted animals, with rodents and primates contributing to about 12% each. They also noted that larger-bodied species represented more than half the total hunted biomass. Furthermore, most species were snared and were generally terrestrial herbivore-frugivores. Finally, the authors concluded that abundance was the main predictor of harvest level.

While there is a general consensus that hunting at unsustainable levels is devastating, the relationship between density reduction and degree of threat is not a simple one because some species may persist at low densities after hunting (Bowen-Jones and Pendry 1999). Some authors have conducted studies to specifically quantify the effects of hunting on vertebrate communities and found the effects to be pervasive. For example, in Brazil, it has been shown that species residing in fragments are more vulnerable to hunters because colonists who farm on

the edge of fragments also hunt for subsistence within fragments (Cullen et al. 2000). Dramatically, ungulates were as much as 69% less abundant in heavily hunted sites. Furthermore, this same study found that species that can persist under heavy hunting pressures in continuous forest tracts become depleted or extirpated in forest fragments. This indicates that population dynamics of hunted species are linked to the size of forest where they reside. The authors also noted that the social organization of individual species can affect how the population as a whole responds to hunting pressure. For instance, the collared peccary is not as socially cohesive as the white-lipped peccary. Hence the collared peccary is less vulnerable to hunting and does not decrease in abundance in heavily hunted areas because hunters kill fewer individuals at the same time. In contrast, up to 80 of the more social white-lipped peccaries have been killed at one time, essentially decimating a whole group with one day of hunting. It appears that susceptibility of species to overhunting increases in fragmented landscapes (Cullen et al. 2000). Confounding this factor, a lack of immigration from productive source areas increases the probability of extirpation especially when local reproductive rates fail to match harvest rates.

Other research confirms the dramatic change in the vertebrate community that occurs as a result of overhunting (Peres 2000a). As hunters selectively target different vertebrate assemblages, Peres writes, "Vertebrate assemblages at forests sites exposed to increasingly heavier hunting pressure were dominated by small-bodied species, which accounted for a substantially lower crude biomass…" (2000a: 248). Larger vertebrates are associated with long generation time and low fecundity and these variables contribute to their being particularly sensitive to hunting. In addition, areas that are only persistently hunted, rather than heavily hunted, show depressed populations of these large vertebrates. The long generation time and low fecundity of larger vertebrates confound their depressed populations as recovery to a viable

population level is not likely (Peres 2000a). Peres's study stresses the effects of selective overhunting on the vertebrate community structure.

As discussed above, hunting can have enormous impacts on the abundance of local populations of vertebrate species. This particular anthropogenic disturbance can also reverberate at other trophic levels and eventually affect tropical forest dynamics and the physical structure and architecture of the forest community. For instance, plant population dynamics that rely on seed disperal by large frugivores may be disrupted by severe population declines in these dispersers due to unsustainable hunting practices (Chapman and Chapman 1995, Peres and van Roosmalen 1996). Furthermore, plant populations have also been documented as being disrupted as the number of large gramnivores and herbivores decline due to hunting because these vertebrates mediate competitive interactions through selective seed predation and seedling browsing (Dirzo and Miranda 1991, Terborgh and Wright 1994). In addition, forest plant and tree communities experience direct physical disturbance caused by large forest mammals that are habitat "landscapers" (Peres 2000a).

In addition to the effects of overhunting on the vertebrate and plant communities of tropical forests, game vertebrates are often a critical resource for tribal and nontribal peoples throughout the tropical world (Melnyk and Bell 1996). Moreover, it has been noted that game vertebrates have been considered a limiting factor to population growth and cultural development of Neotropical indigenous societies (Gross 1975). Selectively overhunting vertebrates may therefore have socioeconomic impacts for local people as it may reduce the value of forests and their ecotourism value. These factors may reduce local indigenous support for retaining primary forest as a land-use option if it is in reality an 'empty forest.' Game hunting is "the single most geographically widespread form of resource extraction in Amazonia and can affect the core of

even some of the largest and least accessible nature Reserves (Peres and Terborgh 1995). Researchers argue that no area accessible on foot within 10 km of the nearest navigable river or perennial stream is safe from hunting, especially as firearms and outboard motors become increasingly affordable (Peres and Terborgh 1995). Tropical communities, including the human community, are dramatically affected by overhunting of forest animals.

Similar conclusions are found in the Congo Basin in Africa (Wilkie and Carpenter 1999). The authors found that duikers, pigs, primates, and rodents are the most commonly hunted groups of animals in the forest. Duikers are the most heavily harvested and these authors focus on this group of species to measure not only how much duiker bushmeat is harvested but also the catchment area that the hunters use. It has been argued that short-lived species such as the duiker should not be harvested at a rate exceeding 40% of its annual production (Robinson and Redford 1991). Some estimate that at only 2 of 12 study sites in the Congo Basin are duikers harvested (Wilkie and Carpenter 1999). In an assessment of hunting impacts, snare trapping by hunters in settlements located along Reserves is having a severe impact on forest animals (Wilkie and Carpenter 1999). There appears to be a positive relationship between yield and distance from settlements (Wilkie and Carpenter 1999). In addition to a better yield, as hunters travel away from settlements, there is increasing wastage of bushmeat left in traps to rot; some hunters left traps unchecked for as long as 77 days. This practice yields 29-39% of wastage. The authors observed that only 11% wastage occurred in traps set closer to the villages. Finally, they conclude that overharvesting of bushmeat is unsustainable for most primates and large-bodied forest duikers and may only be sustainable for highly fecund species such as rodents.

While human hunting is the most obvious in its immediate decimation and elimination of both individuals and populations, there are other proximate anthropogenic effects that are equally

devastating if not quite as dramatic. Disease can play an enormous role in the survival, or lack thereof, in both individuals and populations in the wild.

1.1.1b Parasites and Disease

While infection and disease are a natural part of any population of organisms, it has become increasingly obvious to biologists that human interaction with wild populations has promoted interspecies disease transmission. This issue has implications across several disciplines including the survival and extinction of endangered species. For example, several bird species in Hawaii have gone extinct after being exposed to microorganisms first with the arrival of the Polynesians and then of western civilization (Atkinson et al. 1995). Indeed, several researchers propose that during the last 40,000 years many of the large mammal extinctions were due to "first contact" interactions with humans and their domesticated animals as they expanded globally (MacPhee and Marx 1997, Nunn and Altizer 2006). In terms of primates, there are two well documented cases that illustrate the sobering consequences of disease epidemics in wild populations and how this is a rising concern for conservation biology. First, the presence of Ebola in African ape carcasses depleted some populations by more than 90% illustrated how a combination of bush meat hunting and Ebola poses a clear danger to wild ape populations (Walsh et al. 2003). Second, close proximity to humans infected with polio may have been the cause of an epidemic of paralysis in chimpanzees in Gombe (Goodall 1986, Wallis and Lee 1999). Currently, a growing number of emerging infectious diseases poses significant threat to wildlife populations including rabies, canine distemper, and rinderpest that in the past have only been problematic for domesticated animals (Nunn and Altizer 2006).

1.1.1c Exotic Domestic Animal Predation

Not only can exotic domestic animals pose a threat to wildlife via disease transmission, they can also harm wildlife via predation. Unleashed dogs and feral cats are becoming the chief predators of many species, sometimes far more effective than the species' natural predators (Burkey 2003, McLennan et al. 1996). These exotic species have caused massive extinctions on islands both historically and prehistorically and remain a potent threat to native wildlife despite the explosion of research documenting the disastrous consequences of exotic species (Donlan et al. 2003, Groombridge et al. 1992). For ring-tailed lemurs in Madagascar, encounters with exotic domestic dogs are becoming increasingly common and deadly, with at least several eye-witness accounts of dog predation (Gould and Sauther, 2007, Sauther, 1989, Whitelaw et al. 2007, Millette pers.comm.). In addition, groups are regularly chased or stalked by feral cats and dogs disrupting their patterns of normal travel and resource acquisition. Furthermore, injuries in the lemur groups (some presumably related to the subsequent disappearance of a few of these animals) ranged from broken tails, to open wounds with organs visible, to damaged limbs that impaired mobility (see Chapter 8). In another recent publication, Brockman et al. (2008) argued that domestic dogs and feral cats are becoming increasingly important predators of the diurnal lemurs. According to their reports, feral cats have emerged very recently as a major predator of *Propithecus* at Beza Mahafaly Special Reserve because all of the victims they encountered had died since 2000. The endemic predator, *Cryptoprocta ferox*, is rarely seen, but sightings of feral cats are relatively common (Brockman et al. 2008, Whitelaw et al. 2007). As human influence on natural landscapes becomes increasingly prevalent and populations continue to expand, the baggage that humans carry, namely introduced carnivores such as feral dogs and cats, will expand their roles as predators of endemic wildlife.

1.1.2 Indirect Anthropogenic Effects – *Changes in the suitability of habitat.*

Several researchers argue that the changes in habitat suitability for wildlife have their origins in human population growth and resource consumption (Cowlishaw and Dunbar 2000, Shaw 1989). It has been shown repeatedly that forest loss, habitat degradation, and human density are inextricably linked. For instance, in the Ituri Forest, zero population increase allowed for indefinite forest use with rotating crops. This scenario kept the forest cover intact and did not reduce it by more than 30% (Wilkie and Finn 1988). In contrast, as human population increased by 5% annually, the same researchers recorded a decrease of primary forest patches, an increase in forest clearing, a shortening of the fallow periods for fields, with the consequence of the crop areas having to be completely abandoned after 80 years (Wilkie and Finn 1988). In other parts of the globe, the story remains the same. In Latin America, Asia, Africa, and Madagascar areas of high population density are linked with areas of intensive deforestation and decreasing forest coverage (Barnes 1990, Green and Sussman 1990, Palo 1994). Cowlishaw and Dunbar (2000) observe that while these studies "are conducted at a range of spatial scales and across different geographic regions, they consistently find that human population pressure is the best predictor of tropical deforestation rates" (p. 196). Taking a step back and observing the larger picture of anthropogenic disturbance clearly demonstrates that human population growth, and its resulting demand for resources, is the ultimate basis of habitat loss and degradation.

Focusing in more closely draws us nearer to the details of how anthropogenic disturbance affect biodiversity. The indirect effects of humans' use of forests and wildlife habitat reverberate through the daily lives of animals. Conservation researchers have identified several variables that affect habitat quality – degrading the suitability of habitat - for wildlife in anthropogenically altered landscapes. These include well-identified issues such as fragmentation and degradation,

edge effects, matrix substrate, seedling recruitment, physical stresses to forests, invasive species, and community effects. While these mechanisms of habitat loss and degradation are well-known and identified, what remains largely unknown are the mechanisms by which these issues affect wildlife populations and can lead to local population extinction depending on the species' extinction risk and vulnerability to habitat perturbations.

1.1.2a Habitat Degradation

Research has shown that while it appears superficially to be less devastating than the outright denuding of forest land (i.e. fewer forested acres are converted to non-forested land), fragmentation and degradation is more subtle and insidious (Sechrest and Brooks 2002). Furthermore, when parts, of the natural environment are removed or altered (extractive processes), degradation of habitat occurs. As a consequence, the habitat is less suitable for some organisms that have evolved to the pressures of an undegraded environment. Many human processes and activities contribute to habitat degradation including heavy human or livestock usages, extraction of resources, crop irrigation, and managed natural fire suppression (Sechrest and Brooks 2002). Commonly, these extractive and anthropogenic driven processes drive the degradation process further into habitat fragmentation. Important to remember is that natural habitats have inherent heterogeneity (Sechrest and Brooks 2002). Humans, however, have drastically increased heterogeneity through extractive and habitat conversion processes, which have led to the unnatural isolation of habitats. This isolation and fragmentation has resulted in several complicated problems including decreased area of undegraded habitat, edge effects, habitat islands, decreased dispersal capability, and genetic isolation. Degradation and fragmentation upset the structure and function of an ecosystem and decrease the ability of

species with large home ranges or specific resource requirements to survive (Sechrest and Brooks 2002).

Human land-use practices often result in fragmented patches of remnant vegetation embedded within an agricultural, logged forest matrix, or other developed land (Andersen et al. 1997, Donovan et al. 1997, Gehring and Swihart 2003, Goosem 1997, Laurance and Bierregaard 1997, Saunders et al. 1991). Typically, habitat degradation and fragmentation leads to decreased habitat patch size, higher edge:interior ratios, patches become more isolated, and the degree of connectivity between the habitat patches varies (Gehring and Swihart 2003). This type of habitat and environmental modification can alter the spatial structure of vertebrate populations (Noss and Csuti 1997).

Degraded habitat fragments have often been likened to habitat islands (Simberloff and Abele 1976a, Simberloff and Abele 1976b, Simberloff and Abele 1982, Wilson and Willis 1975). Their isolation from other habitat islands has been the subject of much debate in the literature. This debate mostly surrounds the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) and its applicability to conservation of these forest remnants. The most extensively discussed aspects in the literature include the importance of size, shape, and design of single reserves and reserve systems, extinction and colonization rates, and species-area relationships (Saunders et al. 1991). While these topics are of theoretical interest in examining fragmentation, they are of little practical value in understanding how habitat degradation and the resulting fragmentation effects species on an individual basis and, hence, how to conserve species in fragmented and degraded habitats (Hobbs 1988, Margules 1987, Margules and Stein 1989, Zimmerman and Bierragaard 1985). For example, the species-area equation may give a wildlife manager an estimate of how many species will be maintained in a

forest fragment, but the equation yields no information on which habitats are most likely to maintain species richness and diversity and which resources are key to the viability of populations in these fragments.

1.1.3 Consequences of Unsuitable habitats

Components and variables of degraded and fragmented habitats can vary substantially from their counterparts in continuous and undegraded forests (Murcia 1995, Ries et al. 2004, Saunders et al. 1991). Consequently, these differences have effects on the viability and sustainability of the entire community, including wildlife populations.

1.1.3a Microclimate

i. *Fluctuation of Energy Balance*

There are three key elements that change in the microclimate in degraded ecosystems (Saunders et al. 1991). The first is the fluctuation of energy balance. As native vegetation is removed, the change in architecture and phenology results in an increase of solar radiation during the day and increased re-radiation at night. The biological consequences of this change in energy include a different suite of species occupying the edge of the fragment where the energy change is most dramatic. Soils are also affected by an increase in heat from the increased exposure to the sun and this in turn affects soil microorganisms and invertebrates by disrupting temperature-sensitive processes such as hatching and foraging times. Finally, larger animals are also affected both directly and indirectly through altering resource availability due to the changes in plant growth and phenology.

ii. *Wind*

Wind is the second key element that alters the microclimate of fragments. Forest remnants are more exposed to wind than they were in their native state (Saunders et al. 1991).

This can result in damage through direct physical damage or indirectly through increased evapotranspiration. Windthrow damage results in changes in vegetational architecture and allows increased recruitment, particularly of pioneer and light-demanding species. Increased evapotranspiration occurs as forest remnant edges are exposed to hot, dry winds increase tree mortality via desiccation of humidity-sensitive vegetation, and decrease recruitment for species that require persistent soil moisture or adequate soil moisture.

iii. *Water Flux*

Water flux is the third key microclimates effect of fragmentation (Saunders et al. 1991). Removing native vegetation (for instance removing deep-rooted perennials and replacing them with shallow-rooted crops) changes rates of rainfall interception and evapotranspiration, and hence soil moisture levels. Most commonly, this practice increases erosion as the hydrological system becomes less able to absorb extreme run-off events during rainy seasons. The authors also commented that remnants at the edges of rivers will be more affected that those at the tops of ridges. Ulimately, these changes in the water regime can affect phenology of forest remnants and hence, the fauna in these fragments.

1.1.3b Isolation

i. *Time Since Isolation*

Following the three key changes in microclimates of forest remnants, isolation is one of the three major consequences of fragmented landscapes (Saunders et al. 1991). The biotic response to fragmentation is determined by three key elements including the time since isolation, the distance between adjacent remnants, and the degree of connectivity between remnant forest habitats. Upon isolation, a forest remnant is most likely to have more species than it can support and as the effects of fragmentation begin to appear, species will be lost. This is recognized as

'species relaxation.' This process is an inevitable consequence of fragmentation as area is lost and isolation increases. This process is also predicted by island biogeographical theory. 'Species relaxation' affect different taxa differently. For example, the most rapid species declinates will be those species that are highly dependent on native vegetation, those that require large home ranges, and species that exist at low densities. Dispersal behavior and demography will determine the response of individual response to fragmentation. Populations that are too small to be viable may persist for long periods simply due to long life spans. Time since isolation is an important measure for biologists to understand how far down the 'relaxation track' (Saunders et al. 1991: 23) a forest fragment has traveled. Long isolated remnants can be expected to have lost a significant portion of their original species, and also gained invasive species that are able to thrive in disturbed habitats. Thus, both species composition and species abundance are crucial measurements for evaluating the biological diversity in a remnant area. In conclusion, studying areas disturbed by fragmentation is an important method of examining the process of adaptation.

ii. *Distance from other Forest Remnants*

The second key element of isolation discussed is the distance a remnant is located away from other remnant forest patches (Saunders et al. 1991). The ability of a species to colonize a remnant ultimately depends on its ability to travel the distance to another remnant or area of native vegetation. Colonizing ability is directly related to dispersal mode (Saunders et al. 1991). Other barriers aside, wind-dispersed and highly vagile species are more likely to arrive successfully at another viable habitat. The index of success for such species, however, is highly tied to the how these colonists traverse the matrix habitat between areas of native vegetation. Saunders et al. (1991:23) argued that species may have the physical ability to come to the ground

and disperse long distances, but "lack the behavioral repertoire to traverse the matrix surrounding the remnant; the matrix becomes an effective barrier to movement." In conclusion, different species will react and respond differently to the creation of new groups and detailed knowledge of an organism's behavioral ecololgy is vital to predicting its response to isolation.

iii. *Connectivity*

Connectivity is the third key element in a species' reaction to the isolation effect of fragmentation (Saunders et al. 1991). Corridors, or remnant strips of native vegetation connecting fragments of forests, provide many benefits including enhancing the likelihood of biotic dispersal, extra foraging areas, and refuges during disturbance. Several studies have indicated that corridors appear to increase the likelihood of dispersal for a subset of species that inhabit forest fragments. On the other hand, they can also be corridors for the spread of disease, invasive species, fire, increased predation, and they have high edge: interior area ratios. Indeed, the authors noted, as with many aspects of fragmentation, the merits of corridors and their characteristics are dependent upon the target species. Moreover, the predictions of corridor value must be made with detailed data on how individual species move throughout the landscape.

iv. *Effects Due to Changes in the Surrounding Landscape*

How changes in the landscape surrounding forest remnants affects isolation of species is the final element discussed in this review (Saunders et al. 1991). Logically, fragmentation leads to the concentration of mobile species in forest remnants. These remnants are the only suitable habitat remaining for biota displaced by clearings. As a result, crowding and supersaturation occur which can lead to unnatural inter- and intraspecific interactions. Crowding and supersaturation leads to competition and potential predatory interactions; fecundity may be

decreased leading to a population collapse. Furthermore, crowding can lead to overexploitation of resources that may be unsustainable depending on fragment size. Whereas supersaturation in the forest remnants is a consequence of native species overwhelming the remaining habitat, "there are also potential influxes of new suites of species that have increased in abundance or established in the surrounding landscape following fragmentation" (Saunders et al. 1991: 24). These species can include introduced species such as pasture and crop plants and livestock, and native species that are opportunistic and can exploit the new fragmented habitat conditions. How much a fragment is susceptible to invasion depends upon several variables including how far disturbance factors extend to the interior from the edge. Dispersed by wind or feces species can establish deep with a fragment. The authors also noted that for vegetation, Nonnative species tend to establish themselves where disturbance has occurred, especially if the disturbance has enhanced a limiting resource such as a light gap in a dense forest, or soil nutrient input. Invasive species can also change the landscape within a remnant forest dramatically through grazing which results in changes in the vegetation structure and regeneration pattern. In conclusion, changes in the surrounding landscape, namely introducing crops or livestock, can alter the ecological regime within the forest remnant (Saunders et al. 1991).

1.1.3c Modifying Influences of forest degradation – landscape level changes

i. *Remnant Size*

Finally, the last major characteristic and consequence of degradation and fragmentation are the modifying influences that fragmentation has on the landscape (Saunders et al. 1991). Three key elements that warrant discussion in this section including remnant size, shape, and position in the landscape. The smaller a forest remnant, the greater the influence of external factors on biotic and abiotic components within the fragment habitat. Larger remnants have a

larger core area and are thus less susceptible to the detrimental forces of edge effects. Moreover, larger remnants usually contain greater habitat diversity than smaller ones. Forest fragmentation is rarely random and usually occurs on a selective basis for the best soils, best grazing, best timber, or best wood fuel. Beneficial effects of larger forest remnants include the ability support larger population sizes, which, in turn, tend to have higher levels of heterozygosity. Detrimental effects of larger forest remnants include the possibility of spreading disease throughout an entire population. The effects of remnant size are largely species-specific and species-specific research is required to address the needs of individual species in terms of what they can tolerate and what type of remnant will best support a viable population.

ii. *Remnant Shape*

Remnant shape is only important for smaller fragments of native habitat (Saunders et al. 1991). Indeed, it determines the perimeter:core, or edge:interior ratio. For example, long and thin strips of native habitat have proportionally more edge than either square or round forest remnants. Some native habitats are naturally this shape, gallery forests for instance. Linear strips may also cross high biodiversity environmental gradients and may contain more vegetation types and habitats than the same area in the shape of a square. Species-specific research is necessary to determine the best type of shape for a Reserve if pre-planning of forest fragmentation is necessary and to determine how different species fare when faced with detrimental edge effects.

iii. *Position in the Landscape*

Remnant native habitat is affected by its position in the landscape (Saunders et al. 1991). For instance, the authors emphasize how an undisturbed forest is the construct of its geomorphology, hydrology, and soil composition. Hence, altering the surrounding native

vegetation affects the run-off, or run-on, pattern of a forest remnant. Specifically, a new hydrological regime affects the remnant by changing the movement of soil, nutrients, and seeds that pass into and out of the forest remnant.

Research before 1991 provided few answers to issues of management and what exactly happens to species in fragmented areas (Saunders et al. 1991). Using both single-species studies that can produce results with direct practical application *and* community/ecosystem that may produce more ambiguous results are needed (Saunders et al. 1991). Specifically, the following four issues should be addressed in research: 1.) Understanding the effects of edge effects, particularly comparing intact and fragmented areas; 2.) How internal and external processes interact in a forest remnant and how internal processes have changed since fragmentation; 3.) How isolation is affecting biota within a fragment, particularly the rates of genetic change, genetic variability, and dispersal through both matrix habitat and corridors; 4.) Research has benefited from theoretical studies, but there is a pressing need for field experimentation in management, restoration of fragmented landscapes, and simply collecting species-specific data in these fragments to add to our collective knowledge.

The literature has emphasized the design of nature reserves when fragmentation is discussed (Saunders et al. 1991). In practice, it is usually too late to do anything but try and maintain the remnants that are left following landscape conversion from forest and native habitats to fragmented, degraded systems. Research should shift from focusing on the biogeographic explanations for patterns of species loss to focusing on the externally driven dynamics affecting biota in the fragments (Saunders et al. 1991). In conclusion, there is a pressing need for examining and approaching fragmented and disturbed habitats from the landscape perspective, instead of focusing on separate fragments.

1.1.5 Matrix

Another crucial aspect to be evaluated in any degraded landscape is the matrix. The matrix, or remaining landscape of surrounding fragments, usually consists of a variety of types of land, such as livestock pasture, agriculture, downed vegetation from timber extraction, villages or other structures, small kitchen gardens, secondary forest, mixtures of agro-forestry (homogeneous wood plots), and slash and burn areas. The effects of different types of matrices are important variables to take into consideration when examining the ecology of fragments. Indeed, "no two fragments experience the same effects in part because each fragment is located in a unique section of the altered landscape with random localized habitats and topography remaining" (Marsh 2003, p. 3). Moreover, the matrix is a key variable in the evolution of fragmented landscapes because it behaves as a semi-permeable filter, selective for certain species, for movement between fragments and other landscape features (Gascon et al. 1999, 2000). What is more, species that are adapted to disturbance and can tolerate lower quality habitats will utilize the matrix. Hence, they are capable of invading forest patches and edge habitats. These authors argued that the matrix type can influence the severity of the edge effects in fragments.

It is to their benefit when species can utilize the matrix surrounding a habitat fragment. This facilitates dispersal and access to food resources in other fragments. Species that are intolerant of matrix habitat are more likely to do poorly in fragmented landscapes. Indeed, a "significant, negative relationship between matrix tolerance and extinction proneness for 16 species of rainforest mammal; species that used or exploited the matrix often remained stable or increased in fragments, whereas those that avoided the matrix declined or disappeared" (Laurance 1991: 81). Matrix tolerant species have three important advantages: 1.) they can

disperse between fragments, or between continuous forest and fragments, and therefore increase genetic viability of the population; 2.) they can recolonize fragments following local extinctions; and 3.) since they tend to be generalists, they often exploit ecological changes in fragments, like edge effects, successfully (Laurance 1994). Species that are able to negotiate the matrix habitat are more likely to have long-term viability in a fragmented environment (Marsh 2003).

1.2 Theoretical Frameworks to Understand Habitat Degradation and its Consequences

Degraded habitats and fragments are the result of anthropogenic practices such as logging, hunting, and agricultural habitat conversion. As discussed above, the effects of logging and hunting on wildlife populations have been well documented, and the effects of agriculture to a lesser extent. What is less well understood, and more important to have species specific information, are these more insidious and highly variable anthropogenic activities (Caro 1997). Specifically, with these activities, a species' habitat is altered in a way that affects their resource base. The resources may still be available, however, they maybe more fragmented, scarce, and embedded in matrix habitat. Critical to a species' persistence in this type of habitat is the flexibility of their ecology and their ability to use remnant forest habitats. Saunders et al. (1991: 19) argued, "over much of the world, conservation of regional biotas depends entirely on the retention and management of these remnant habitats. Conservation managers are therefore faced with the dual issues of whether the remnant forests have any practical conservation values, and if they do, of how they must be managed to retain these values."

The fact that human land-use practices often result in degraded patches of remnant vegetation embedded within an agricultural, logged forest matrix, or other developed land has been well documented (Gehring and Swihart 2003, Saunders et al. 1991, Laurance and Bierregaard 1997, Donovan et al. 1997, Goosem 1997, Andersen et al. 1997). Typically, habitat

degradation leads to decreased habitat patch size, and higher edge: interior ratios; patches become more isolated, and the degree of connectivity between the habitat patches varies (Gehring and Swihart 2003). This type of habitat and environmental modification can alter the spatial structure of vertebrate populations (Noss and Csuti 1997).

1.2.1 Island Biogeography Theory and Metapopulation Theory

Degraded habitats and habitat fragments have often been likened to habitat islands (Diamond 1975, May 1975, Simberloff and Abele 1976a, Simberloff and Abele 1976b, Simberloff and Abele 1982,Wilson and Willis 1975,). Their isolation from other habitat islands has been the subject of much debate in the literature. This debate mostly surrounds the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) and its applicability to conservation of these forest remnants. The most extensively discussed aspects in the literature include the importance of size, shape, and design of single reserves and reserve systems, extinction and colonization rates, and species-area relationships (Saunders et al. 1991). With communities, Island Biogeography Theory (IBT) (MacArthur and Wilson 1963, 1967) models species richness on oceanic islands depending on the influx of colonization and the extinction rate on the island. By extension, the oceanic island can be likened to a forest habitat remnant. The extinction rate in an island population, and the colonization rate, vary according to the size of the island and distance (area and isolation) to the mainland, respectively (Irwin 2006). Furthermore, the extinction rate increases as the number of different species rises (species richness) while the colonization rate decreases due to the likelihood that good dispersers are already present on the island. Thus, an equilibrium is present between colonization and extinction based on species richness. Below the equilibrium the island will accumulate species

based on the colonization rate, and above that number, the island will lose species according to the extinction rate – all based on the island's size and distance to source populations.

Until recently, island biogeography theory structured much of the research to predict how fragmentation would affect species numbers (MacArthur and Wilson 1967, Shafer 1995, Wilcox 1980). In addition researchers used the theory to debate the effect of fragment size and the impacts of reserve size (e.g., SLOSS; single large or several small Reserves: Bierregaard and Lovejoy 1986, Bierregaard and Dale 1996, Gilpin and Diamond 1980, Harris 1988, Lovejoy and Bierregaard 1990, Redford 1992, Saunders et al. 1991, Simberloff and Abel 1976ab, Soulé and Wilcox 1980). While these topics are of theoretical interest in examining fragmentation, they are of little practical value in understanding how fragmentation affects species on an individual basis and, hence, how to conserve species in fragmented and degraded habitats (Hobbs 1988, Margules 1987, Margules and Stein 1989, Zimmerman and Bierragaard 1985). For example, the species-area equation may give a wildlife manager an estimate of how many species will be maintained in a forest fragment, but the equation yields no information on which habitats are most likely to maintain species richness and diversity and which resources are key to the viability of populations in these fragments. Furthermore, IBT treats all species on an even playing field, ignoring interspecific differences in tolerating habitat degradation and its associated challenges, including dispersal ability. In addition, the theory assumes that habitat types are far more simple than the complex set of variables that exists in reality. It assumes that there are large mainlands, supplying large source populations, and small islands. In reality, interspecific differences in species persistence and resource availability in degraded habitats and the matrix between habitat remnants, all contribute to the variables involved in potentially predicting species survival.

Therefore, IBT may predict the extinction rate, but cannot predict which species may be more at risk in degraded habitats (Irwin 2006).

Metapopulation theory was first described as modeling a "population of populations" (Levins 1969, 1970). More recent research has expanded this definition and described metapopulations as a group of subpopulations that are typified by migration among the subpopulations. Models have also expanded to include multiple species (Holyoak et al. 2005, Horn and MacArthur 1972, Nee et al. 1997). The subpopulations, or local populations, are groups of individuals utilizing the same habitat (Hanski 1998, Hanski and Gilpin 1991, 1996, Hanski and Simberloff 1997, Marsh 2003). These definitions detail the subpopulations as identical, spatially separated populations in suitable (undegraded) habitat patches that are divided by a matrix of unsuitable (degraded) habitat. While the habitat patches are suitable for occupation, they are not necessarily continuously occupied, meaning local extinction may occur. Furthermore, a true metapopulation is self-sustaining based on the dynamic flow of colonization in unoccupied patches. This flow can be described as movement between 'sinks' and 'sources.' Most modeling and theoretical research indicates that metapopulations operate with this source-sink dynamic (Pulliam 1988, Schlichting and Pigliucci. 1998, Turelli 1997). In this situation, source populations typically occupy a source habitat characterized by high quality resources. Moreover, source populations tend to recruit more individuals that than they lose and thus offer potential migrants. Sink populations, however, tend to occupy poor quality habitats and tend to lose more individuals than they can recruit. Sink populations can emigrate from a higher quality habitat into a lower quality habitat, such as a fragment, and subsequently do poorly over the long term (Chapman et al. 2003, Van Tienderen and Koelewijn 1994.). In areas where the matrix is hostile and unsuitable for travel for some species, subpopulations may become locally adapted to

their specific resource base as a result of the lack of flow between populations (Templeton and Georgiadis 1996).

Current studies have shown that the metapopulation perspective can be a valuable paradigm for studying the ecology of habitat loss and degradation (Marsh 2003, Sanderson and Harris 2000, Sih et al. 2000, Wiens 1996). For example, identifying and examining the dynamics of survival in sink habitats may offer insight into species' adaptive responses and species persistence in degraded habitats. Indeed, probing into the variables of declining habitats, or sinks, may address the limits of adaptive evolution (Irwin 2006, Wilson and Yoshimura 1994). Crucial to understanding how metapopulations are organized at the regional level is knowing where source and sink populations are located and the basic behavioral ecology data of how species react in degraded habitats (Irwin 2006, Rodriguez-Vargas 2003). Furthermore, with focused research in sink habitats, researchers may be more apt to understand evolutionary innovation (Slatkin 1985, Van Tienderen 1991). This is especially true in sink habitats where habitat deterioration is gradual and with moderate immigration to provide genetic variation, adaptive evolution would be more likely (DeWitt et al. 1998, Kawecki 1995, Sih et al. 2000, Sultan and Spencer 2002). Metapopulation researchers have also suggested that organisms may respond to habitat degradation and fragmentation via 'enhanced dispersal' (Sih et al. 2000, Wilson and Yoshimura 1994). Specifically, species may disperse more, and perhaps differently than they would in a pristine and undisturbed landscape, as a result of the new ecological pressures resulting from fragmentation. The majority of these ideas and theories have not yet been examined in the wild. Regardless, they provide insight into how researchers can use the metapopulation ecology paradigm to ask new questions and approach important conservation issues that will prove essential to field investigations investigated.

Research has indicated that when a metapopulation approach is combined with landscape ecology, population dynamics, and behavioral ecology it can prove to be a viable, significant, and important foundation for conservation (Marsh 2003, Wiens 1996, Sanderson and Harris 2000). However, the metapopulation approach can be problematic when researchers apply it to rapidly changing habitats (Chapman et al. 2003, Lawes et al. 2000, Thomas 1994). Metapopulation theories are based on the idea that stochastic fluctuations in local populations cause local extinctions and thus unoccupied habitat patches are available for recolonization. Yet, in most degraded landscapes that are fragmented by agricultural plots or logging practices, local extinctions occur due to increased levels of deforestation and habitat conversion that degrade the habitat to the point that it is uninhabitable for species. Thus, recolonization is not possible. Applying metapopulation theory to "on the ground conservation" proves to be limited due to the stark contrast of degraded habitats not offering suitable habitat patches for recolonization. The earliest models also lack sophistication of realistic variables: habitat patches were assumed to possess the same chance of extinction and colonization. In reality, there are important inter-patch differences and variables that cannot be ignored such as the ability to disperse across the matrix, appropriate resource base, and potential predators to name a few. As this discussion has illustrated, metapopulations provide a more dynamic avenue for variables than Island Biogeography Theory models by incorporating more comprehensive variables into their models and using data driven dispersal rates and species habitat requirements to procure more accurate predictions. At the same time, incorporating these more sophisticated models require intimate knowledge of the behavior, ecology, and other species characteristics. Like Island Biogeography Theory, metapopulation models are also overly reliant on the assumption of classifying habitats as suitable or Non-suitable, when in reality there are more gray areas, not a simple dichotomy

(Irwin 2006). True metapopulation models, while useful in visualizing the regional dynamics of populations in degraded landscapes, are likely to be extremely rare in the wild (Harrison 1994). Thus, metapopulations have a higher potential to predict species persistence, sustainability, and potential extinction in degraded, fragmented, and disturbed habitats. However, they most likely rarely exist in the wild and the level of detailed data required to accurately predict situations preclude their application in all but the most well known habitats and species (Irwin 2006). While these theories are problematic, using them as frameworks to gain a broader understanding of how a species can persist in degraded habitats is valuable in obtaining insight into the broader dynamics of landscape ecology including how species use the matrix surrounding degraded habitats and the ability of species to disperse.

1.3 Primates in Anthropogenically Disturbed and Degraded Habitats – what does the research tell us?

Unprotected lands in the tropics are providing scientists ample avenues to explore and investigate the dynamics of anthropogenically induced habitat disturbance. As these complex ecosystems unravel, "the vast adaptations and interdependencies that may elude us within intact forests are being systematically deconstructed within fragmented landscapes" (Marsh 2003: 2). To the detriment of the occupants, forests are rarely anthropogencially modified with an eye toward their future ecological requirements. Be it natural or anthropogenic, habitat degradation disrupts ecologic processes because of variables such as edge effects, the nature of the matrix, fragment size, available resources, and the location of the habitat in the greater ecological landscape (Laurance 1997, Saunders et al. 1991). Multiple studies have shown that bird, mammal, and insect communities respond differently to disturbance, and have different degrees of survival based on the perturbations to their required resource base (Bierregaard et al. 2001, Laurance and Bierregaard 1997, Laurance et al. 2002). Recently, researchers have cited that one

of the most potent threats to primates is anthropogenically induced habitat disturbance: especially fragmentation, degradation, and deforestation (Chapman and Peres 2001, Cowlishaw and Dunbar 2000, Marsh 2003). Due to the variable responses of primates to habitat modification (Chapman and Peres 2001), a critical examination of primate responses to habitat modification is vital. This examination is not only critical from a primate conservation perspective, but also inherently interesting due to the process of adaptation and changing ecology that is occurring and can be documented as species are facing challenging ecological and environmental conditions (Saunders et al. 1991).

1.3.1 Effects of anthropogenic habitat disturbance on primates

i. Behavior, ecology, demography

Studying the distribution, abundance, and demographic composition of primates inhabiting anthropogenically disturbed landscapes is a critical element for understanding the dynamics and conservation needs of a species (Marsh 2003). There are two distinct phases in which species respond to habitat degradation and disturbance (Wilcove et al. 1986). During the first phase, individuals will attempt to adjust to the habitat modification via behavior. In the second phase, changes from the first phase reverberate and trigger modifications in the demographic composition of the group and, hence, the population. The modifications during the first phase include alterations to activity budget, feeding, and ranging behavior (Cowlishaw and Dunbar 2000; Johns 1986,1987, 1988, 1991, 1992; Johns and Skorupa 1987, Marsh 1981). These adjustments in turn affect the social behaviors: time spent grooming, playing, socializing. These behaviors are pivotal for maintaining relationships within primate groups (Cowlishaw and Dunbar 2000, Marsh 2003). It is only until very recently that researchers have begun to focus on the consequences of anthropogenically induced habitat disturbance on the sociality and behavior

of vertebrates (Marsh 2003). This is likely due to the difficulty of extrapolating data from populations in isolated and disturbed habitat fragments to the broader landscape population level (Yahner and Mahan 1997). Moreover, it can be challenging to argue a causal relationship between habitat variables and behaviors. To diagnose habitat disturbance induced behavioral phenomena, it is critical to use the comparative method and study species in both fragmented and relatively undegraded environment habitats (Yahner and Mahan 1997). Demographic variables of groups are more easily collected during brief census and survey studies, while behavioral ecology of fragmented species calls for longer-term studies (Marsh 2003). Despite these challenges to understanding the behavioral and ecological dynamics of primates in fragmented landscapes, research into these issues is timely and urgently needed (Chapman and Peres 2001).

1.3.2 Are there ecological correlates of tolerance and behavioral flexibility in primates in anthropogenically disturbed habitats?

i. *Behavioral and Ecological Modifications in disturbed habitats*

Interspecies differences are often quite variable, even when occupying the same habitat and especially when examining the probability of survival (Bierregaard et al. 2001, Irwin 2006, Laurance and Bierregaarrd 1997, Laurance et al. 2002,). Some of these conclusions are unsurprising. For instance, that forest dependant, large-bodied predators with extreme ranging patterns go extinct in forest remnants separated by anthropogenically disturbed habitat while some smaller animals with limited ranging capability persist, is predictable (Irwin 2006). While this example may be straightforward, the myriad of animals with differing ecological variables between these extremes are not as effortlessly explained.

Relatively few studies have examined the impacts of anthropogenic habitat degradation on primate communities, but the finding that primate species vary in their responses to changes

in habitat is a consistent theme running throughout this research (Chapman and Peres 2001). Even when habitat variables and species assemblages are controlled for, researchers have found conflicting results. Historically, researchers have conducted most long-term primate studies in intact, undisturbed forests (Irwin 2006, Marsh 2003). This method makes sense on several levels: 1.) evolutionary adaptations that have been unaffected by human practices should be clear; and, 2.) there is a higher chance that catastrophic human activities (hunting, clear-cut logging) will eliminate the study population (Irwin 2006). With this strategy, however, current primatology, pressured with significant and imminent conservation threats is ill equipped with data describing alterations of primate behavior and ecology in disturbed habitats. Earlier studies attempted to reveal specific characteristics that statistically explain the persistence of species in modified habitats (Johns and Skorupa 1987, Skorupa 1986). For instance, Skorupa (1986) determined that susceptibility of primates to habitat disturbance increased as the following three factors increased: 1.) average group spread; 2.) percentage of fruit, seeds, and frugivory; 3.) home-range size. Johns and Skorupa (1987) found that frugivory and body size both served as good predictors of persistence ability in disturbed habitats. These studies concluded, perhaps prematurely, that frugivory and body size both served as good predictors of persistence ability in disturbed habitats (Johns 1986, Johns and Skorupa 1987). In contrast to a previous postulate that body size would be a strong predictor of a primate species' survival ability (e.g. Wolfheim 1983), results indicated that the effects of body size approach statistical significance only when the effects of diet type are controlled (Johns and Skorupa 1987). Moreover, research indicated that smaller bodied species coped with disturbance more successfully and the degree of frugivory in a primate's diet was negatively correlated with population persistence in degraded habitats. The strongest conclusion indicated large-bodied frugivores were the most sensitive to habitat

disturbance. As more studies have been conducted, the obvious variability in primate species' responses to disturbance has increased (Irwin 2006). Conflicting results make it increasingly challenging to draw conclusive and effective conservation strategies.

Successional forests and agricultural practices that result in a mosaic of differently aged forests can be key for primates to survive in disturbed landscapes. For example, groups of spider monkeys inhabiting habitat fragments surrounded by a matrix of slash and burn agricultural plots appear to have similar behavioral ecological traits with the same species in continuous forests (Ramos-Fernández and Ayala-Orozco 2003). In a study of two groups in slash and burn induced fragments in the Yucatán, spider monkeys were found to have similar social organization, home range size and proportion of fruit in the diet as found in studies of *A. geoffroyi* in continuous forests. Groups in the agriculturally embedded habitat fragments successfully exploited successional forests as well as primary forest fragments. The main source of habitat disturbance in this area is slash and burn agriculture, and agricultural plots are left to recover and regrow, resulting in a mosaic of heterogeneous forests. Contrarily, forests that are converted to large areas have much larger degraded areas and less heterogeneity in forest succession. In the grazing produced fragments, spider monkeys tend to experience local extinction. On the other hand, spider monkeys in smaller degraded habitats in the Yucatán, are able to utilize the secondary successional forests to travel to other areas, disperse, and utilize other patches of fruiting trees. This appears to be a key variable in persistence of this species (Ramos-Fernández and Ayala-Orozco 2003). Even more important, these groups appear to have a net increase in their population, indicating not only success in resource acquisition, but reproduction as well. Understanding the behavioral ecology of habitat use in this species may provide insight into how

to construct or plan for habitat corridors that might include patches of agricultural, rather than large and open pasture land.

There have been conflicting results in studies examining frugivorous feeding and persistence in anthropogenically modified habitats. For instance, results have indicated that smaller frugivores fared relatively well in degraded forests compared to larger frugivores and folivores (Fimbel 1994). Contrarily, two separate studies examining the effects of logging disturbance on the primate assemblage in a dipterocarp forest in peninsular Malaysia and in Borneo revealed entirely different conclusions (Bennett and Dahaban 1995, Johns 1992). In Borneo, logging resulted in an immediate and drastic decline of the gibbon and langur population from 35 to 70%. In stark contrast, in Malaysia, the same species suffered only a 10% decline and some populations grew by 74%. Clearly, there are other complicating ecological variables influencing the disparate responses of these primates. While large-bodied frugivores appear to be the most sensitive to habitat disturbance and body size and the degree of frugivory were the strongest negative correlations with survival, there may be too much variation in primate responses to accept this conclusion (Chapman and Peres 2001, Johns and Skorupa 1987). Exceptions to this rule include a healthy and viable population of howler monkeys that exists in a severely degraded habitat that had been both logged and grazed (Chapman et al. 2000). Similarly, groups of common chimpanzees have been documented in areas that were logged and almost completely converted to agriculture. These populations are successful due to their ability to travel between the remaining habitat fragments and raiding crops (Naughton-Treves 1996). Very recently, Johnson et al. (2005) reported that orangutans, a large-bodied frugivore, are thriving in disturbed forests at only slightly lower densities than in primary forests. Clearly, conclusions regarding ecological correlates of survival or population persistence in primate

species are difficult to find and perhaps variation in the response of primates to disturbance is the only conclusion. These studies and results indicate that variability is the rule, not the exception. Species success may be tied intimately to the site's ecology and both the type and degree disturbance (Fimbel 1994).

Several researchers have indicated that there are two distinct phases in which species respond to habitat fragmentation and disturbance (Wilcove et al. 1986). During the first phase, a species will attempt to adjust to the habitat modification via behavior. In the second phase, changes from the first phase reverberate and trigger modifications in the demographic composition of the group and, hence, the population. During the first phase, behavioral modifications include alterations to activity budget, feeding, and ranging behavior (Cowlishaw and Dunbar 2000, Marsh 1981, Johns 1987, Johns and Skorupa 1987). In turn, these modifications affect social behavior, such as time spent grooming or playing, behaviors that are integral for maintaining relationships within the group (Cowlishaw and Dunbar 2000, Marsh 2003). It is only until very recently that researchers have begun to focus on the consequences of habitat degradation on the sociality and behavior of vertebrates (Marsh 2003). This is partially due to the difficulty of extrapolating data from an isolated fragment population to the broader landscape population level (Yahner and Mahan 1997). Moreover, it is challenging to argue a causal relationship between habitat variables and species' behaviors. To diagnose behavioral phenomena induced by habitat degradation, it is imperative to use the comparative method and study species in both fragmented and relatively undegraded habitats (Yahner and Mahan 1997). This challenge is compounded by the fact that demographic variables of groups are more easily collected during brief census and survey studies, while behavioral ecology of fragmented species require longer-term studies (Marsh 2003). Despite these challenges to understanding the

behavioral and ecological dynamics of primates in fragmented landscapes, research into these issues is timely and desperately needed (Chapman and Peres 2001)

Until recently, very few scientists have directly or indirectly focused on the consequences of habitat fragmentation on the behavioral ecology and behavioral flexibility of primates (Marsh 2003). Orangutans in both logged and unlogged forests have shown some of the behavioral ecological changes rendered through selective logging (Rao and van Schaik 1997). Results indicated that orangutan densities were 40% less in the selectively logged habitats. In fact, individual orangutans avoid logged forests if they have an option of traveling in unlogged habitats. Activity pattern analysis indicated that orangutans spent more time traveling in the logged habitats, and significantly less time resting. There were also differences in feeding behavior. For instance, individuals spent more time eating fruit in the unlogged habitats and more time eating leaves in the disturbed, logged forest. It appeared that there was a shift toward folivory in logged forests even though phenologically, fruiting rates remained constant in logged forests. Locomotion was also affected by the structural changes to the forest. Individuals tended to use more energy-expensive locomotion in the logged forests. The shift in diet and locomotion seemed to be qualitatively linked to the fact that logged forests offered more spatially clumped and smaller food patches and young leaf production may have been higher. The resulting decline of orangutans in logged areas relates to a decline in a specific type of fruit, soft-pulp fruits, that appear to be less abundant in the logged forests. Orangutans exhibit some behavioral flexibility in logged forests (Rao and Van Schaik 1997), however it is dependent on the type of logging that occurs. This example indicates that primates can compensate for certain degrees of habitat perturbation. Furthermore, documenting examples of flexibility can help direct and inform management of local, site-specific logging and agricultural practices.

Several species of howler monkeys have been relatively well studied in terms of the behavioral effects of habitat degradation, specifically fragmentation (Bicca-Marques 2003, Rodriguez-Luna et al. 2003, Silver and Marsh 2003). For example, in two experimental studies, howler monkeys were released into habitat fragments (Rodriguez-Luna et al. 2003, Silver and Marsh 2003). Two main conclusions can be drawn from the results of these studies: 1.) howler monkeys appear able to exploit novel food items and switch to new food items when others become more scarce due to rising population levels; and 2.) howler monkeys appear to make behavioral adjustments that seem to minimize energy expenditures. With these behavioral and ecological modifications, howler monkeys are able to persist in habitats with variable food abundance. The behavioral changes include adjusting time budgets for resting and foraging. Fragment size was not linked to howler monkey ecology and behavior in terms of their day range, main food general selected, activity budget, or the number of plant species consumed daily (Bicca-Miques 2003). It does, however, predict home range size, the number and diversity of leaf and fruit species in the diet. While it may appear from the behavioral flexibility noted in these species, howler monkeys do not appear able to persist long-term in habitat fragments (Bicca-Marques 2003, Juan et al. 2000). Bicca-Marques argued that, "despite their ability to survive in forest patches with few and minor changes to their behavior, they are still vulnerable to hunting, disease, and predation (p. 294). He also argued that not enough information is available to make these generalizations genus-wide. Bicca-Marques concluded by saying, "we urgently need comparative studies analyzing the behavior of particular species under varying degrees of habitat fragmentation" (p. 294). By examining species in previously intact fragments, researchers can "reduce the influence that different floristic compositions may have on the resulting patterns" (Bicca-Marques 2003 p. 294).

In a larger study in Brazil, Chiarello (2003) argued that several species of Atlantic forest primates exhibit "a high degree of ecological flexibility and adaptability" (p. 117). He measured two variables: 1.) the success of primates determined by their density, and 2.) the sizes of their surviving populations in forest fragments of various sizes. The six main primates in this area are muriquis, holwers, capuchins, masked titi, marmosets, and lion tamarins. Chiarello found that these species are subject to a number of external and internal factors that negatively affected their survival. These factors included edge effects, fire intrusions, selective logging, and illegal hunting. Internal factors negatively affected these primates included competitive and predatory interactions, and encroaching edge effects. Contrary to other studies, Chiarello argued that his data indicate that overall primate abundance within fragments showed no clear relationship with fragment area or hunting pressure. Furthermore, this result supports his assertion that these primates exhibit a "high degree of behavioral flexibility and adaptability" (p. 117). He concluded by stating that "it is evident that the problem of fragmentation has become much more complex than when originally conceived" (p. 116). Furthermore, due to this complexity, it is increasingly difficult to generalize results and extrapolate the effects of fragmentation from studies carried out in different localities. Chiarello argued that to create the most effective understanding of fragmentation, studies in the future must have a more local approach to truly realize the complexity of the local landscape matrix and biological idiosyncrasies of the organisms.

1.4 Primate Studies with Theoretical Frameworks:

1.4.1 Do Primates fit the metapopulation model?

There have been relatively few studies applying metapopulation theory to primate populations. Consequently, results have shown mixed responses within primate populations

(Irwin 2006). For example, Chapman et al. (2003) noted that metapopulation models were helpful in interpreting data, even though species did not show increasing probability of incidence with increasing patch area and decreasing incidence with a patch's degree of separation. This was especially true in several studies of *Cercopithecus ascanius, Procolobus badius*, and *Pan troglodytes* that observed their mobility between patches (Chapman 2000, Chapman et al. 2003, Onderdonk and Chapman 2000). Accordingly, these observations tend to reduce the effects of isolation and patch area on a species ability to persist (Irwin 2006).

Some research has indicated that metapopulation models may be valuable in determining the health and viability of a species at a landscape model. For example, using subpopulation data for squirrel monkeys and then extrapolating the results for unknown populations, yielded strategies for conservation and management at a site in Panama (Rodriguez-Vargas 2003). Specifically, Rodriguez-Vargas (2003) used "empirical evidence of movement patterns and predications of increased movement patterns under environmental conditions of scarce resources" (p. 55). Using ArcView software, he determined the maximum probable radius of dispersal, the probability of dispersal through the matrix, and devised a model of population persistence for squirrel monkeys. For well-studied species, using metapopulation theory may help determine colonization from source populations and elucidate persistence probabilities in some habitats.

Cowlishaw and Dunbar (2000) asserted that while there are some studies beginning to use metapopulation theory, little is known about primate metapopulation dynamics. With only a few primate species studied under the metapopulation dynamics paradigm – and the majority of these studies using empirical evidence from one habitat to extrapolate extinction rates for populations in unrelated habitats - primatologists have a long road before developing conclusive

results. Despite the lack of comprehensive application of metapopulation to primate populations, Cowlishaw and Dunbar argued that eventually these data will be useful to determine what ecological variables buffer species against extinction if they have a low extinction rate. Furthermore, understanding which species have high extinction rates alerts researchers to examine what makes various primate species more prone to extinction in particular systems. Their research suggests that rescue effects associated with metapopulations have also received little attention in the primate literature, but there is evidence that they may play a key role in the persistence of subpopulations. Populations doomed for extinction are 'rescued' by the immigration of individuals from neighboring populations. Furthermore, with the variety of locomotor patterns among primates, terrestrial versus arboreal primates and quadrupeds versus more specifically adapted leapers, the ability to transfer between populations and 'rescue' populations across varying matrix substrates will prove vital for many primate populations' persistence. Cowlishaw and Dunbar (2000) cited several examples where this phenomena occurs. Among the diurnal primates, the rescue effect seems to be important in reducing the extinction rates in both red colobus and crested mangabeys in the fragmented habitat surrounding the Tana River. For black-and-white colobus monkeys, gully habitats in Ethiopia appear to have fewer key resources than gallery forests. Monkeys inhabiting these more marginal gully habitats are 'rescued' by overflow from source populations in the gallery forest. Similarly, Cowlishaw and Dunbar noted that in gelada populations above 4,000 meters, growth rates can drop below zero. They argue that populations lower down the mountains grow as much as 13% per year and that the higher elevation populations are only able to persist because of 'in-migration' from the lower source populations. Clearly, these dynamics are important to understand for species that

are failing to thrive in marginal habitats. A metapopulation approach offers a unique perspective on how to examine primates in neighboring, but disparate habitats.

However, the majority of metapopulation studies indicate mixed responses, surprising results among primate species, and no clear pattern of which species might fare better in degraded, fragmented habitats (Irwin 2006). For instance, the Tana River National Primate Reserve in eastern Kenya is a well-studied gallery forest composed of habitat patches. There are three species of endemic primates at these sites: Tana River red colobus (*Procolobus rufomitratus*), crested mangabey (*Cercocebus galeritus galeritus)* and Sykes' monkey (*Cercopithecus albogularis albotorquatus*) (Anderson et al. 2008). Modeling the metapopulations of these primates revealed that mangabeys have a higher ranging requirement, and higher colonization rates for both Sykes' monkeys and red colobus than the mangabeys. Ecologically this is unexpected because the mangabeys are well known to be the most terrestrial of these species (Irwin 2006). Furthermore, the model predicts that the colobus has a higher probability of extinction in larger patches, whereas mangabeys have the highest risk of extinction in smaller patches. The latter result is understandable due to the requirements of frugivores and home ranges. Despite some of the models' unsurprising results, they only receive mixed support from researchers' data on extinctions, colonizations, and species persistence in the wild (Anderson et al. 2008). The models are inconclusive until long-term data corroborate their predictions.

Another example illustrates the failure of metapopulation theory predictions to match the incidence of primates in disturbed habitats. Lemur incidence in 11 habitat patches surrounded by a deforested matrix in eastern Madagascar did not correlate with the predications of metapopulation dynamics (Dehgan 2003, Irwin 2006). In this comprehensive study, species

richness did not vary with the size of the habitat patch. There was no predictive pattern to correlate the patch size with the number of species. Furthermore, species richness increased with increased distance between patches and between patches and continuous forest.

Chapman et al. (2003) argued that metapopulation models can be problematic when applied to rapidly changing habitats. They stated, "metapopulation theories are based on the idea that random fluctuations in local populations cause local extinctions and thus unoccupied fragments are available for recolonization" (p. 75). Yet, in most fragmented landscapes, local extinctions occur due to increased levels of deforestation and habitat conversion to pasture or agriculture that degrade the habitat to the point that it is uninhabitable for primates. Thus, recolonization is not possible. Other authors have acknowledged these limitations of metapopulation models (Lawes et al. 2000, Thomas 1991). When comparing primate metapopulation models to those for other mammals, primates appear to not fit the metapopulation theory as well. For instance, in a mixed species study involving Samango monkeys, hyrax, and duikers in forest fragments in South Africa, the researchers found that while the incidence models matched their survey data well, Samango monkey incidence varied only with patch area, not with patch isolation distance, nor with any other ecological variables (Lawes 1992, Lawes et al. 2000). This was in sharp contrast to the hyrax and duiker whose incidence correlated positively with area, inversely with isolation distance, and was also linked with some ecological variables (Irwin 2006). From these data, it appears that duikers and hyrax persist in a mainland-island metapopulation dynamic with colonization rates equalling extinction rates, while the Samangos do not. This example brings insight to a critical dynamic of examining primates in degraded habitats – they may not disperse similarly to solitary species. Indeed, because of the "strong centripetal force" of group dynamics, Samangos may not disperse

as well as duikers and hyrax (Irwin 2006, Lawes et al. 2000). Commonly, emigration involves lone individuals dispersing between groups (which may deter the emigrant from crossing a problematic matrix solo) or group fissions that results in the emigration of the subordinate subgroup (cf. Cords and Rowell 1986). As a result, unoccupied patches will not experience recolonization and metapopulation models will fail to predict adequately the dynamics for some primate populations. Another critical component that further complicates using primate populations in metapopulation modeling, is the relatively long intergenerational time characteristic of primate life history patterns. Extended life history stages may "cause a lag time between habitat changes and distributions" (Irwin 2006). These complicating factors may be disguising relationships between patch area, isolation distance, and dispersal.

1.4.2 Do Primates fit the Island Biogeography Theory and its predictions?

Primate researchers have not focused on applying Island Biogeography Theory to studies. As a result, there are very few studies that have tested the predications of IBT in primate populations (Irwin 2006). In general, the results are varied and suggest that IBT is not adequate to explain the dynamics of primate species incidence in fragments. For example, Onderdonk and Chapman (2000) note that the patterns of incidence of nine primate species in degraded habitat fragments near Kibale National Park, Uganda, increase in species richness as patch size increases, however, species' incidence patterns are not significantly related to either area or isolation distance. In Gabon, results of another study examining eight primate species in degraded habitat patches illustrated a similar lack of predictive power from the Island Biogeography Theory (Tutin et al. 1997). The incidence patterns with these species showed no effect of isolation on the presence of a species in a habitat patch indicating that this population does not follow the predictions of Island Biogeography Theory (Irwin 2006). Conversely, in

India, researchers were able to positively link area and species richness with lion tailed macaques, thus supporting IBT with a primate study (Umapathy and Kumar 2000, 2003). Finally, in Madagascar, Deghan (2003) studied the species richness of twelve lemur species in several habitat patches. Not only did species richness not correlate significantly with patch area or distance, but primates were observed traveling between the patches. This violates predictions of IBT, where travel would occur only between the 'mainland' and 'island' habitats, not between 'island' habitats. From these examples, we can presume that IBT is not adequate to explain the intricacies, variability, and flexibility that primates exhibit in terms of incidence and species richness in habitat patches that are a result of anthropogenic habitat alterations. Irwin (2006) proposed several reasons for these discrepancies: (1) primates' ranging and traveling patterns are inconsistent with Island Biogeography Theory's structure of individuals' inhabiting patches with little to no dispersal; 2.) research thus far demonstrates that primates tend to travel and disperse between patches, rather than strictly between the mainland continuous forest and habitat patches; 3.) primates' susceptibility to poor habitat variability; and, 4.) research thus far has described several situations of observed distributions representing Non-equilibrium situations (Irwin 2006).

1.4.3 Habitat Quality and Primate Species

The theoretical models discussed above are limited in that they use habitat area and isolation as the only variables to predict incidence and abundance of a species. Primates, however, have been clearly documented as particularly flexible in both behavior and ecology – some primate species more than others. If these well described models cannot adequately explain primate species abundance and incidence, then perhaps there are more complicated, and less easily documented variables that may elucidate patterns of abundance and incidence in degraded habitats (Irwin 2006). While several studies have begun to test this hypothesis with

varying results, it is perhaps the beginning of primatologists being able to describe the larger picture of primate population success. For example, while the number of food trees present had no effect on three primate species in one study in Kibale (Onderdonk and Chapman 2000), subsequent data demonstrated a convincing relationship between food availability and presence of colobines in the same area (Chapman et al. 2004). Researchers have linked high incidence of colobines with a high protein:fiber ratio in degraded habitats. This result indicates that carrying capacity is actually higher in degraded habitat patches that are able to produce high plant biomass (Irwin 2006).

In the Tana River area, an analysis of red colobus monkey distribution found correlation between habitat characteristics and incidence probability (Mbora and Meikle 2004). Specifically, abundance of food trees, the amount of habitat edge, and species composition, were strongly linked to the presence of red colobus. This study also indicated a lack of correlation with habitat patch area. Furthermore, research examining mangabeys in the same degraded region demonstrated that basal area of mangabey food sources and explained the abundance of mangabeys in habitat patches (Wieczkowski 2004). Moreover, mangabeys frequently travel terrestrially through degraded matrix to habitat patches indicating that metapopulation theory may be inappropriate to describe the dynamics of this species. These lines of evidence point to a stronger relationship between habitat quality and presence of primates, rather than habitat geometry dictating primate incidence.

Further compounding the evidence that primate incidence is more adequately explained by habitat quality than habitat geometry are several studies of tamarins in habitat patches in Brazil (Gilbert 2003, Rylands and Keuroghlian 1988). In this research, tamarins were more commonly seen in smaller habitat patches, suggesting a positive correlation with edges and

secondary forests: a positive edge effect (Rylands and Keuroghlian 1988). Since the earlier research, it has been documented that tamarins and saki monkeys have had more successful, persisting populations in patches surrounded by unburned matrix, thus subsisting in habitat patches surrounded by significant secondary forest regrowth (Schwarzkopf and Rylands 1989). Moreover, these species utilize resources in the matrix and travel through it to use resources in the continuous forest. Again, characteristics describing habitat quality had stronger correlations to primate incidence and population success than simple patch dynamics.

Research examining macaque (*Macaca silenus*) and langur (*Trachypithecus johnii*) incidence in forest patches in India found several habitat variables that predicted the incidence of both species (Umapathy and Kumar (2000a, b). Specifically, macaque presence was positively correlated with tree height, while langur presence was positively correlated with tree density. When the researchers added more habitat variables to help describe the patterns of incidence, predictability did not improve. These results imply that habitat quality, rather than variables such as area, is the key resource for these species (Irwin 2006).

Samango monkeys also show patterns of incidence that are correlated with both plan species richness and habitat patch area in non-continuous forests in South Africa (Lawes 1992, Lawes et al. 2000). Patch isolation, however, is not correlated with this species' incidence. This finding indicates that while area may be an indicator for the pattern of incidence for Samango monkeys, plant species richness is also linked and one of the primary variables for discussing both IBT and metapopulation theory, namely isolation, is not related to samango monkey incidence indicating the lack of robusticity for these theories with another primate species.

Finally, a comprehensive study in Madagascar studied the effect of botanical and animal community effects on the patterns of lemur populations in 11 forest patches in the eastern rain

forests (Deghan 2003). The number of lemur species present in forest habitat patches was not linked to plant species richness, food resource abundance, area or isolation of the habitat patch, or predators. Primary habitat quality variables, such as structural forest variables and variation in plant species composition were not examined in this study which might be the primary link to lemur species' abundance and measure the level of habitat disturbance. In this landscape, and with the comprehensive nature of this study examining 11 species, it is a powerful indicator that neither area nor isolation explains the variation in species incidence. Indeed, it appears that there are other measures of habitat quality, besides the variables that are used in both IBT and metapopulation theory, that are the primary indicators for primate species' incidence in habitat patches (Irwin 2006).

1.4.4 Habitat Quality between Suitable Habitats – The Primate Matrix

Largely overlooked in primate studies, but perhaps a key ecological variable in rapidly changing habitats, is the matrix between areas of suitable habitat (Jules and Shahani 2003, Rickets 2001). A convincing non-primate study illustrates the compelling potential of investigating this variable. Laurance (1990) comprehensively examined five nocturnal folivorous marsupial populations in ten habitat fragments, seven control sites, and three corridors connecting the fragments. The study's landscape variables included area, elevation, shape index, topographic diversity index, time since isolation, linear distance to continuous forest, linear distance to nearest fragment >20 ha, length of the corridor connecting the forest, and length of the largest non-continuous habitat in the corridor. Results indicated that three variables predicted marsupial species richness: richness varied positively with area, negatively with corridor disjunctions, and negatively as isolation measures increased. Interestingly, these species appear to follow IBT and metapopulation predictions (Irwin 2006). Like primates, the five marsupial

species varied in their response to the degraded habitats: some species did not differ in abundance between control and fragment habitats, whereas others were rare in fragments and corridor habitats but existed at higher densities in less degraded, continuous forests. A key analysis in this study was Laurance's (1990) attention to dispersal ability and correlated it to probability of extinction. No primate study to date has considered dispersal ability (between degraded habitats) as a correlate of proneness to extinction (Irwin 2006). Laurance (1990) found that dispersal ability index was significantly negatively correlated with vulnerability. This relationship indicates that species that use matrix habitats are least prone to extinction. Indeed, metapopulation models, and the "rescue effect" hypothesis are consistent with this finding (Brown and Kodric-Brown 1977, Hanski 1994, Lomolino 1986). Furthermore, other non-primate studies have yielded similar results (Gascon et al. 1999, Laurance 1991).

While perhaps difficult and yielding low incidence of observations, examining the dispersal and matrix use behavior among primates may help explain the observed variability in primates' tolerance of degraded habitats (Irwin 2006, Jules and Shahani 2003, Rickets 2001). Several studies, while not focusing on quantifying matrix habitat use and tolerance, have hinted that primates vary in their tolerance and ability to disperse and use matrix habitats and that this might indeed be a key variable to predicting survival (e.g. KwaZulu-Natal: Lawes et al. 2000; DBFFP: Lovejoy et al. 1986; Kibale: Naughton-Treves et al. 1998; Rylands and Keuroghlian 1988, Swart and Lawes 1996; Anamalai Hills: Umapthy and Kumar 2000a). In fact, indirect evident from several primate studies lends support to the idea that primates that are successful in negotiating matrix habitats may also have lower extinction probabilities (Irwin 2006). For example, 75% of the primates with the highest observed incidence in degraded forest habitat fragments in Kibale, also appear to cross matrix habitats (Naughton-Treves et al. 1998,

Onderdonk and Chapman 2000). Furthermore, Naughton-Treves's (1998) crop-raiding study illustrated that *Cercopithecus ascanius*, the species with the highest observed fragment occupation incidence and tolerance, is commonly observed raiding agricultural plots (matrix habitat) surrounding the Kibale's continuous forest blocks.

Currently, primatologists have no direct studies to consult regarding this potentially important factor. Irwin (2006) has suggested that future primate studies should critically examine two specific variables: 1.) Diversity in matrix characteristics; and, 2.) correlates of primate use in, and tolerance of, matrix habitats. Specifically, matrix habitats are extremely variable: cattle pasture, plantations, and other disturbed habitats with varying degrees of habitat regrowth. In addition, mutiple factors shape the matrix habitat including local abiotic and biotic conditions, seed dispersal sources, anthropogenic activity and density. Indeed, both structural and floristic diversity will determine resource availability and mortality risks for animal species. Moreover, these variables will determine the propensity of animals to disperse through, forage in, or cross matrix habitats (Irwin 2006). Studies should also examine and collect data on which primate species are more tolerant of the challenges in matrix habitats. Specifically, primatologists need documentation on whether matrix usage is random or if there are links to body size, diet, social behavior, locomotor patterns, or broader community patterns, such as predator assemblage. Other mammalian studies have indicated the value and importance of dispersal in disturbed habitats to species' persistence, the significance of matrix structure characteristics, and metapopulation survival (Aberg et al. 1995, Didham and Lawton 1999, Fitzgibbon 1997, Laurance 1990, 1991; Mesquita et al. 1999, Thomas 2000, Tilman et al. 1994). Irwin (2006: 24) pointed out that it is critical for primatologists to realize the "importance of matrix use to persistence in fragmented landscapes, and quantify the structure and composition

of matrix, and its use during ranging and dispersal." Each of these factors speaks to the magnitude of including the landscape perspective when examining primate populations, and for primatologists to acquire insight into, not only what primates are doing in undisturbed habitats, but how they are negotiating challenges in degraded habitats with direct observations of ranging and dispersal behaviors.

1.5 Summary of Primate Studies in Degraded Habitats – Compounding Complicating Factors

Studies that examine primate persistence and population success in degraded habitats are rife with complicated ecological variables. Furthermore, models designed with less behaviorally complicated species, and a host of anthropogenic variables that pose imminent threats to our closest relatives in the wild because they are too simplistic. The unfailing pattern is the inherent variability that primate species exhibit in degraded habitats (Irwin 2006). Some species are found consistently in disturbed and degraded habitats and fragments, whereas others are not as successful (Ganzhorn 2000a, b, 2003). Just as consistent, however, are conflicting results for predicting which primates will be most successful and can persist in more challenging, degraded habitats. As indicated previously, simple correlations with primate characteristics such as body weight, diet, and locomotion are either highly variable or the results are inconclusive across studies or even in the same study.

In the larger arena of primate conservation, these unclear results have significant consequences for determining the anatomy of primate reserves (Irwin 2006). From current studies, it appears as if primate nestedness is high: small habitats, fragments included, consistently support the same species (Deghan, 2003, Ganzhorn 2000, 2003). From this, primate conservation managers can conclude that small reserves will only preserve a subset of species and may exclude the species that tend to suffer in smaller habitats. Several researchers have

concluded (not for primates, but for most mammalian species) that large reserves will be crucial to preserving primate species (Atmar and Patterson 1993, Patterson and Atmar 1986, Patterson 1987).

Consistently, IBT and metapopulation theory have not garnered convincing support in describing primate populations (Irwin 2006). While they are useful in offering a framework for beginning to examine dispersal and matrix use in primate populations, they should not be relied upon for primate incidence predications. Primates may be too ecologically and behaviorally complicated for the current iterations of these models. Or, primate research may not yet be detailed enough to provide the necessary variables to validate them. What does seem to be interrelated are habitat characteristics and primate abundance (Chapman et al. 2004, Irwin 2006, Mbora and Meikle 2004, Wieczkowski 2004). In several studies, habitat structure and the characteristics of habitat fragments have a more significant relationship to primate persistence, presence, and occupancy than the isolation or area of degraded habitats (Irwin 2006, Mbora and Meikle 2004, Umapathy and Kumar 2000). Adding layers of complexity, it has been suggested that while patch size and isolation are linked to structural habitat variables (Bender et al. 1998), ultimately, habitat characteristics (phenology, tree height, shrubs and herbs) may be the "causal factor behind local extinctions" (Irwin 2006: p. 25). Additionally, preliminary evidence of how primates use degraded, smaller habitat patches show that some species, or, in some cases, site specific populations, do not merely disperse between habitats, but use fragmented habitats as part of their range (Irwin 2006). Perhaps because primates are so flexible and diverse in how they utilize a landscape, as residents of habitat patches or of continuous forest habitats ranging through smaller fragments, traditional IBT and metapopulation models will fail because they do not adequately discuss take into account these compounding variables.

Primate studies tend to be more difficult and time intensive and are comprised of lower sample sizes, making it more elusive to collect data on edge effects, and behavioral and ecological shifts. Butterfly studies, for instance, in degraded habitats and small habitat patches, can be done with rapid censusing. Time-intensive primate studies, however, are essential to teasing apart interspecific differences in population persistence and finally answering the question regarding which habitat variables will correlate to persistence (Irwin 2006). It is likely that because primates are flexible in their responses to habitat variables changing, long-term consequences and patterns may take time to surface.

Another compounding and complicating factor resides in the communities that primates live in and that they rely on explicitly: large tropical trees (Irwin 2006). Primate species are integrally connected with the resources large tropical trees provide: food, shelter, and locomotion substrate. Because most habitat destruction is fairly recent, the effects on forest regeneration from both losing large trees and the browsing of saplings has not been fully realized. Irwin (2006) points out that there will be a "time lag" between habitat destruction and the full effects of habitat alteration on primate ecology. In the meantime, primates are not negotiating the full ecological challenge that awaits them as forest regeneration may not occur if tree reproduction is interrupted by human activities. Forest ecological change at the landscape level will be just as vital as primate behavior and ecology in predicting the persistence of species (Gigord et al. 1999, Irwin 2006).

Ideally, primate conservationists would be able to develop a set of easily and rapidly collected species characteristics that predicted risk of extinction. Each of the studies examined thus far have indicated that only extremely detailed and site-specific data lends clarity to the incidence and persistence patterns in degraded and anthropogenically altered habitats and

landscapes. Combining several behavioral and ecological correlates for a species and the seasonal habitat patterns in degraded habitats might allow researchers to assess the future success of a population in a specific site. For example, knowing the seasonal and spatial distribution of fruit for a frugivore such as an orangutan or spider monkey, along with the resource distribution and structure of a habitat remnant could facilitate predicting the persistence of these species in these specific sites. However, gaining insight into seasonality, behavioral patterns, and resource distribution are long-term projects. Less labor intensive variables and species characteristics, or already known variables, such as body weight, general dietary category, phylogeny, etc. do not offer useful, rich information. Indeed, Chapman et al. (2004) argued that even home range size is an inadequate predictor of species persistence since primate densities consistently vary in degraded habitats, connected to altered food distribution, interspecies competition, and predation pressure.

In conclusion, that primate species vary in their response to habitat perturbations is clear. What is unclear, are the root causes of the variation. By extension, this lack of clarity limits primate conservationists' ability to create realistic conservation plans. Primates whose resources are quickly dwindling, i.e. forest-dependant primates, require research that asks - what are the variables of survival? What are the most potent conservation measures? There are several avenues to approach these questions. In general, comparisons between species inhabiting similar habitats will facilitate teasing apart the variables that define population persistence. For instance, a comprehensive interspecific comparative study of sifaka (*Propithecus verrauxi*) and ring-tailed lemur (*Lemur catta*) in and around Beza – Mahafaly Special Reserve in Madagascar would greatly illuminate the dynamics of large vs. small social groups and frugivore versus folivore dietary patterns, and leaper versus quadruped locomotion adaptations. Furthermore, another

important approach is to examine intraspecific behavioral dynamics in protected habitats and compare these to groups in degraded, anthropogenically altered areas. Indeed, these approaches may prove insightful to understanding the directions of adaptation, as species respond to anthropogenic alterations of habitat (Irwin 2006).

Toward this end, important directions of future primate research include:

i. Examine how primates use habitats at the landscape level: Due to the complexity of primate behavior and intricacy of social relationships, research of primates in disturbed landscapes has lagged behind the quantity of data researchers have already accumulated in protected, relatively unaltered forests. Inter- and intraspecifically, primates utilize habitats very differently, depending on habitat structural variables. In addition, behavioral flexibility to mediate environmental variables is commonly the first line of defense, or adaptation, for primates. Consequently, these sets of variables, landscape features and primate behavioral and ecological differences, warrant further investigation to understand the extent of how primates negotiate their landscapes.

ii. Examine primate population persistence: Obvious causes of primate population decline are well-known; destruction and conversion of primary primate habitat, disease, and hunting. What is less clear, are the mechanisms that lead to extinction and what determines the variability of persistence across taxa. Several researchers have indicated that long-term studies of well-known species in degraded areas will provide valuable insight of the relative potency of each major contributing factor of population decline (Chapman et al. 2005, Irwin 2006).

iii. Integration and development of comprehensive primate population models: The shortcomings of current models, both IBT and metapopulation dynamics, are problematic for primate populations as they overlook several significant primate specific variables: dispersal

ability, matrix use, and incidence patterns not varying consistently positively with patch area and negatively with isolation. Primates appear to have more complicating features that require further investigation.

From this discussion and the work of several researchers, it appears that a more comprehensive model including quantification of patch isolation, habitat quality, and anthropogenic activity would more accurately predict primate incidence (Armstrong 2005, Franken and Kik 2004, Irwin 2006, Krauss et al. 2004, Larsen et al. 2004, Lawes et al. 2000). Models are key tools for conservation managers and policy makers to enact effective and positive decisions regarding species status and measures, and levels, of protection.

iv. Examine the Behavior of Extinction: This discussion has shown that primates are inconsistent regarding their behavior in various habitats. Indeed, that primate species vary in their suite of behaviors in different habitats, and landscapes, is evident (Caro 1999, Irwin 2006, Lima and Zollner 1996, Yahner and Mahan 1997). Examining and interpreting whether behavioral changes become advantageous adaptations, or prove inadequate and drive a population towards extinction, is a critical variable to incorporate into potential models (Anthony and Blumstein 2000). Currently, most models are based on behaviors that are documented in relatively undisturbed habitats. Applying these to primates in altered and fragmented landscapes is not an accurate assessment of the dynamics that occur in the typical primate landscapes. Indeed, primate behavior is a key variable in landscape dynamics. For instance, intertroop encounters can either deter or attract primates from "landing on" occupied pieces of habitats (Irwin 2006). Some species monitor neighboring groups during intergroup encounters and make decisions on the timing and direction of dispersal based on their observations (Pope 1990). Understanding the dynamics of how neighboring groups influence dispersal will be an important behavioral marker

of population persistence. In addition, many authors have suggested that the inherent flexibility in primate social, behavioral, and dietary modes is fundamental to their persistence in degraded habitats (Deghan 2003, Silver and Marsh 2003). A useful tool to incorporate into models and measures of primate persistence is a quantitative measure of behavioral ecological flexibility. Embedded in the measure would be variables capturing the number of behavioral ecological variables and the number of sites where these have been noted (Irwin 2006). To be sure, this process would demand numerous data points and sites to create an accurate model. The results would be invaluable to measuring flexibility and the ability of primates to potentially cope in degraded habitats. Furthermore, conservation planning would be more effective based on increased predictability of primates to cope in anthropogenically modified habitats.

1.6 Importance of Addressing Primates in Disturbed Habitats

Anthropogenic habitat degradation and its consequences such as fragmentation is only one suite of challenges with which primates must cope (Chapman and Peres 2009, Irwin 2006). Hence, preserving habitat is only one part of the solution of the multifaceted and diverse array of threats that the extant primates face. Striving for, and achieving, efficient and wise conservation solutions requires an integrated understanding of primates' adaptive responses to habitat perturbations.

While primates have not been labeled a keystone species, those species whose ecological impact is disproportionate to their impact in their communities, they are perhaps among the most charismatic species in many tropical ecosystems. As such, conservation organizations gain traction using primates as symbols of significant conservation efforts. As a result, organizations can potentially accumulate substantial resources. While not ecologically a keystone species, primates could be labeled an "economic keystone species." Their draw for tourists and

conservation dollars is disproportionate to their biomass in tropical forests. On the same note, preserving primates encompasses preservation of their resources which will preserve countless other plants and animals. Researchers have also noted that primates can play significant roles in maintaining plant diversity and even forest regeneration (Chapman and Onderdonk 1998, Ganzhorn et al. 1999). Preserving primates, therefore, contributes significant impact to larger landscapes and ecosystems.

While not only a necessary factor to prevent primate extinctions, understanding primate conservation, population and community dynamics at the landscape level in degraded habitats can provide primatologists valuable insight into the adaptive responses of primates in challenging landscapes. Maintaining the study of primates in undisturbed forests will continue contributing valuable data substantiating our understanding of primates' natural history. What is perhaps more important today, however, is a "sound understanding of the ecological processes governing extinction" (Irwin 2006: p. 29). Not only will this provide conservationists tools with which to craft effective protocols, but it will expand anthropologists' knowledge of the selective processes at work in degraded habitats.

1.7 Overview of this Study

In this study, I present results from the first comparative study of the behavior and ecology of ring-tailed lemurs (*Lemur catta*) in protected and unprotected habitats. In addition, this study is one of the first in-depth comparative studies of resident primate populations inhabiting anthropogenically degraded forests. From October 2005 through June 2006 I studied four groups of lemurs within the Beza Mahafaly Special Reserve, a seasonal deciduous forest located in southwestern Madagascar. Two study groups are found within one parcel of a well-

established and protected portion of the Reserve, and two lived outside the protected area, in grazed and farmed habitats.

This study is significant in that it contributes to the imminent need for long-term data collected simultaneously on primate groups living in degraded habitats and those living in protected, intact habitats. In addition, it is one of the first long-term comparative studies of primates in degraded, anthropogenically altered habitats. This study's tenure is also important in that it captures the seasonal ecology of Madagascar that dictates important ecological variables that virtually prevents short-term studies of behavior and ecology from being relevant for the Malagasy primates. In addition, previous primate studies, mentioned in the discussion of this chapter, have noted incidence patterns rather than behavior, or compared behavior of degraded habitat dwelling primates to data in other studies. Consequently, this comparative study presents a cohesive and compelling examination of primates in adjacent habitats with differing ecology and habitats.

Chapter Two presents the details of the history of the study site, its size and geography, the lemur population, the local people, and the structure of the protected Beza Mahafaly Special Reserve. This background information is necessary to discuss the details in the following chapters regarding the habitat differences, spatial arrangement of lemur groups, and landscape elements that influence the ecology of this area.

Chapter Three will detail the results of botanical surveys and months of phenological monitoring I conducted within the ranges of each of the four study groups. This chapter details the foundation of forest structure, anthropogenic influences, and resource base in and around Beza Mahafaly Special Reserve (BMSR) and is integral to drawing connections about lemur ecology in anthropogenically altered habitats.

Chapter Four describes the effect of anthropogenically altered habitat on the feeding ecology of *Lemur catta*. I evaluate results from instantaneous data comprised of both plant parts and species eaten. Furthermore, I provide an evaluation of foraging data. I compare Reserve and Non-Reserve Groups in both feeding and foraging and the seasonal differences observed between groups. To provide a comprehensive and historical evaluation of the feeding ecology data, I include previous Beza Mahafaly feeding ecology studies.

Chapter Five examines ranging patterns, height of tree use, fragment use, travel times, travel behavior among the four groups. This chapter broadly examines several aspects of spatial ecology and how these lemurs are utilizing the landscape. I also examine GPS data to estimate home range and day range sizes in the Beza Mahafaly landscape.

In Chapter Six, I investigate whether habitat differences among the lemurs' ranges influences their activity patterns. I compare these data through analysis of instantaneous activity data, active time per day, and each groups' constructed activity budgets.

Chapter Seven examines the intricacies of the four groups' social behavior. I present results using instantaneous data assessing differences in social cohesion, rates of grooming, play aggression and scentmarking.

Chapter Eight examines the effects of anthropogenically altered habitats on population viability, I present preliminary results of reproductive success, predation, and injuries of the four groups in this study. Based on the October through June data, and other anecdotal reports, my results include birth rates, death rates, and infant survival.

Finally, in Chapter Nine, I summarize and integrate the results and conclusions from the preceding chapters. Moreover, I discuss the contributions of study to the overall understanding of how anthropogenically altered habitats can affect primate populations and the importance of

the landscape approach in primate conservation studies. In addition, I present conservation recommendations for the Beza Mahafaly *Lemur catta* population, in addition to broader primate conservation recommendations. Finally, I propose future research directions based on the conclusions made in this study.

CHAPTER 2

PROJECT BACKGROUND, METHODS, AND MATERIALS

2.1 Introduction

2.1.1 Origin of the Project

This study originated as Dr. Sauther and I were walking along a deforested area of former gallery forest beside the dry, Sakamena River in southwestern Madagascar. A dissertation is a long process involving an amalgam of thoughts, ideas, accompanied by some sweat, and tears. As such, it deserves some background – to paint the picture of what happened before the document, during the document, and after. As scientific inquiry does, it began with an observation from a nascent Masters student walking with her advisor in a disturbed gallery forest just outside of Beza Mahafaly Special Reserve and asking questions, "Wow, these lemurs are occupying very disparate habitats – I wonder if they behave differently in these different forests? I wonder if they eat different plants? I wonder if these populations are viable in disturbed habitats? How are they adapting? Are they flexible? And, if so, how?" This project is rooted in the great tradition of anthropology to approach research questions and projects with a holistic view: not only am I examining the species that is the focus of each groups' diet, but I also focus on the landscape level of anthropogenic impacts (agriculture, road systems, domestic dogs, and natural disasters to name a few) that are part of this story of change, adaptation, and survival of the greater BMSR ring-tailed lemur population.

This chapter provides in-depth discussions of several integral topics that are the foundation for interpreting the following data driven chapters. First, I will examine the specific project background that grounds this dissertation in the theory of biological anthropology and how this project fits within this framework. Second, I will provide specific project background,

pilot study results, recent stochastic events, and the observations that led to the questions posed in the following chapters. Finally, I will discuss recent research, events, and pivotal information that will help interpret the results in the full context of the current ecological and research landscape at BMSR.

2.2 Anthropological Theoretical Foundation

Among the living primates, some genera successfully inhabit a wide range of habitats, most notably, *Papio*, *Macaca* and *Homo* (Fleagle 1999). Species' adaptability, its basic biological and behavioral plasticity, explains much of this success (Huss-Ashmore 2000). Today in biological anthropology, such plasticity refers to "the ability of many organisms to change their biology or behavior to respond to changes in the environment, particularly when these are stressful" (Mascie-Taylor and Bogin 1995, p. i.). A fundamental assumption is that organisms that show greater adaptability are those that are more widely distributed; i.e., they are able to exist within a greater range of environments and/or are better able to deal with environmental change. While documenting adaptability in humans has been widely studied (Huss-Ashmore 2000), it has not been a focus of empirical research for wild non-human primates. In fact, much of the work in behavioral ecology has concentrated on primates in relatively undisturbed and protected forests (Bronikowski and Altmann 1996, Cheney and Seyfarth 1987, Fuentes et al. 2001, Grassi 2002, Goldsmith et al. 1999, Isbell et al. 1990, Mutschler 2002, Peres 1992, Sauther et al. 1999). This offers only limited insight into the adaptability and flexibility of organisms, and then only by inference and implication (Caro 1998, Rubenstein 1997, Underwood 1992,Weaver et al. 1996, Wolff et al. 1997,). As Caro (1998) noted, despite the extensive work on primate behavioral research, there remain too few behavioral ecological studies of any species to address the questions of how species adapt to environmental change. Primatologists have long been

interested in primate responses to habitat variation (Dunbar 1987, Jay 1968, Nishida et al. 1983, Rowell 1966, 1967), but only recently, as a result of the conservation crisis for primates, has the research begun to focus urgently on how primates respond behaviorally to habitat fragmentation and disturbance (Marsh 2003). To assess the resilience of an endangered species, one must collect information specific to the flexibility of a species' foraging behavior, demography and their dispersal capacity (Weaver et al. 1996, Wolff et al. 1997). Such information also has important conservation implications. For example, successful conservation of species inhabiting perturbed areas requires understanding of the behavioral responses organisms exhibit in rapidly changing environments (Rubenstein 1997, Underwood 1995).

2.2.1 Understanding environmental adaptation among primates

Primate researchers have begun to examine what specific characteristics enable a species to persist in anthropogenically altered habitats and how it responds to new environmental challenges posed by proximity to human activities (Bennett and Dahaban 1995, Chapman et al. 2000, Chapman and Lambert 2000, Estrada and Coates-Estrada 1996, Fimbel 1994, Ganzhorn 1995, Johns 1992, Johns and Skorupa 1987, Naughton-Treves 1996, Olupot 2000, Onderdonk and Chapman 2000, Skorupa 1986, Tutin 1999). A theme running throughout this research is that primate species vary in their responses to changes in habitat. These authors sought predictive variables of how habitat disturbances affect primates in habitat fragments, but with very limited success. They concluded that more research is needed. For example, one paper argues, that without consensus on the predictive variables of how such disturbances affect primates in marginal habitats, we cannot generalize about primate responses (Onderdonk and Chapman 2000). Similarly, another paper argues that the existing research fails to explain the complex relationship between primate behavioral ecology and habitat disturbance (Chapman and Lambert

2000). Because anthropogenic alterations of habitats pose such severe threats to wildlife in the tropics, conservation managers' frustration is understandable. So also is the urgency that researchers express for investigating, for example, the ecological requirements, dietary flexibility and behavioral adaptability of primates in anthropogenically altered landscapes (Tutin 1999). Finally, in a comprehensive review in *Evolutionary Anthropology* regarding the role of primatologists, the authors contend that due to the complexity of the issue and the contrasting results regarding the responses of primates to habitat degradation, the discipline requires more research on the ecology of primates in disturbed habitats (Chapman and Peres 2000).

2.2.2 Significance and Intellectual Merit

It is my intention that my work will contribute to the theory and discipline of anthropology in three significant ways. First, it will add to the limited literature on the behavioral flexibility of non-human primates in a relevant setting. Anthropologists have characterized both humans and non-human primates as a behaviorally 'plastic' species (Bogin 2001, Box 1991, Fleagle 1999). Moreover, Slobodkin (1968) makes the case that individuals undergoing non-catastrophic environmental stresses react first by behavioral alterations. Subsequently, as variation naturally exists, natural selection may select for physiological adaptations, then, finally genetic adaptations at the population level. Given how quickly habitats can be altered, understanding the first of these, behavioral alterations, is therefore key. However, few data exist on how non-human primates exhibit behavioral flexibility. This study of *L. catta* in anthropogenically-altered habitats provides empirical insight into this process of adaptation. Specific hypotheses have been tested regarding the behavioral flexibility of a primate in a setting that is rapidly changing from anthropogenic disturbance. As a result, these findings can increase

our understanding of the socioecological traits that enable primates to exploit different habitats and adapt to ecological challenges.

Second, this study will contribute directly to the literature on the socioecological correlates of variation in species' responses to habitat disturbance. Several recent papers have emphasized the importance of documenting the contrasting responses of different species to habitat change (Chapman and Lambert 2000, Chapman and Peres 2001, Onderdonk and Chapman 2000). Without such research, our knowledge of primates' ability to respond to, and survive in, anthropogenically altered habitats will remain incomplete, and our diagnoses and prescriptions tentative, filled with more conjecture than effectiveness. The data and findings published from this study will contribute to the as yet too limited empirical inventory available to those whose research focus on primates in fragmented and degraded habitats. The project responds to compelling arguments in the professional literature and urgent appeals at professional conferences and in the conservation media.

Third, this work links ecological research directly with local conservation goals. From a literature review, the trend has been for researchers to develop theories of behavioral ecology primarily based on their observations of primates in relatively undisturbed, and protected habitats. Yet, the subsistence and commercial activities of humans have been devastating intact habitats, leaving anthropologists with diminishing ability and confidence to describe and explain the effects on primates existing within anthropogenically altered and disturbed habitats. Researchers can combine ecological studies with conservation goals to help determine the most effective management plans for endangered species. With specific knowledge of the behavioral adaptations that allow this species to inhabit a wide variety of environments, including those

with more limited resources, and by directly involving local people, conservation and development plans will be more effective.

2.3 The Study Species

Lemur catta, the ring-tailed lemur, belongs to the family Lemuridae of the primate infraorder Lemuriformes (Figures 2.1a,b,c). The genus *Lemur* has only one species, *L. catta.* Closely related extant genera include *Eulemur, Varecia,* and *Hapalemur* (Fleagle 1999). *L. catta* is an opportunistic omnivore with a broad diet (Sauther et al. 1999). Food resources are dramatically seasonal with lowest resource availability during the dry season (Sauther et al. 1999). They live in relatively large, multi-male, multi-female groups (Jolly 1966, Sussman 1992). A clear distinction from most other primates is that females are agonistically dominant to males (Jolly 1966, Kappeler 1990, Sauther 1991). With a short breeding season each year, research documents that reproduction in this species is directly linked to their phenology of resources, most likely to support lactation and weaning of juveniles in their extremely seasonal environment (Sauther 1998). Unlike the majority of lemurs which are restricted to specific habitats, the ring-tailed lemur is found in a variety of environments throughout southwestern Madagascar. This includes gallery, deciduous, dry scrub forests and even high elevation montane habitat (Goodman and Langrand 1996, Mittermeier 1994, Sussman 1972). They thus provide a relevant template for understanding how a primate species reacts to challenging habitats. Researchers have conducted a number of sociological studies on *L. catta*, a 'flagship species' for Madagascar, and their ecology within several Reserves is well-documented (Budnitz 1976, Budnitz and Dainis 1975, Gould 1997; Gould et al. 1999, Jolly 1966, Jolly et al. 2002, Koyama *et al*. 1991, 2001, Sussman 1972, 1991, 1992, Sauther et al. 1999, 2003, Taylor 1986).

The ring-tailed lemur is listed as vulnerable in the IUCN database (IUCN 2004), but its status may be more precarious than that. A recent survey of the range of *L. catta* within southern Madagascar has revealed a pattern of "pockets" of populations within widely disparate habitats

and often separated by areas of inhospitable habitat (e.g. treeless savannah) (Sussman et al. 2003, Sauther and Whitelaw, unpublished data). *L. catta* survival may be linked closely to the persistence of certain types of habitats (Sussman et al. 2003), the decline of which the IUCN listing may not reflect. For example, unprotected gallery forest, a key habitat component for *L. catta,* was harvested at a rapid rate in the early 1990s (Sussman et al. 1994) and that is continuing (Sauther et al. 1999, Whitelaw and Sauther 2003). *L. catta* is unable to return to former population size after being reduced by hunting, and small populations are quite vulnerable to the effects of stochastic events which may lead to reduced gene flow and lowered genetic variation (O'Connor 1987, Gould et al. 1999). Furthermore, the dry and deciduous forests of southern Madagascar that are key ring-tailed lemur habitats are being depleted even more rapidly than the rainforests of the east (Sussman et al. 1994, Smith 1997, Smith et al. 1997, Sussman et al. 2003). Janzen (1988) saves the title of "the most threatened of the major tropical forest type" for tropical dry forests, the primary habitat of *L. catta*. Clearly the habitat of *L. catta* is under anthropogenic assault. Examining the species' response to this habitat alteration is timely and important.

Figure 2.1a Study species with identification collar at Beza Mahafaly Special Reserve.

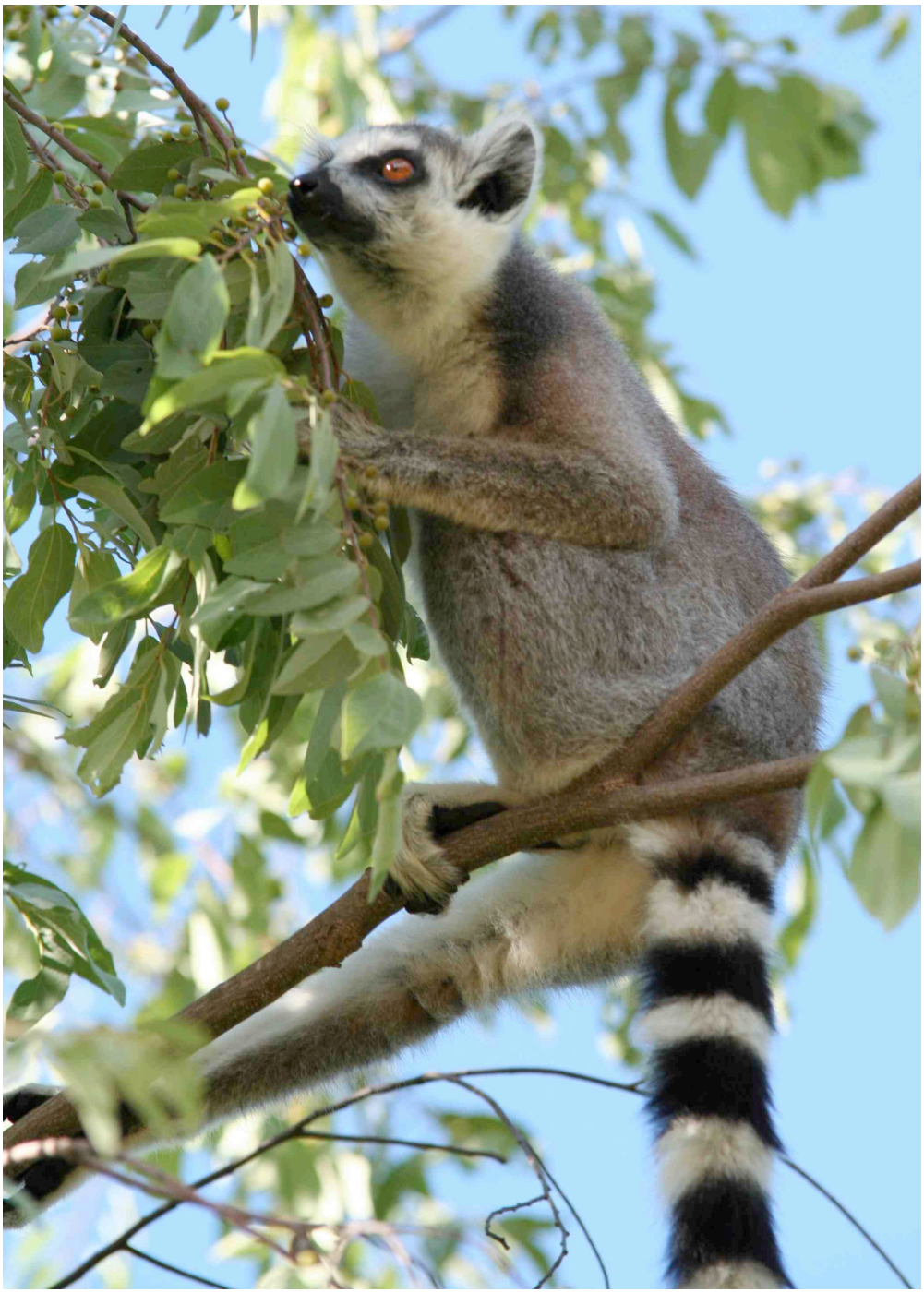

Figure 2.1b *Lemur catta*, the study species, feeding arboreally.

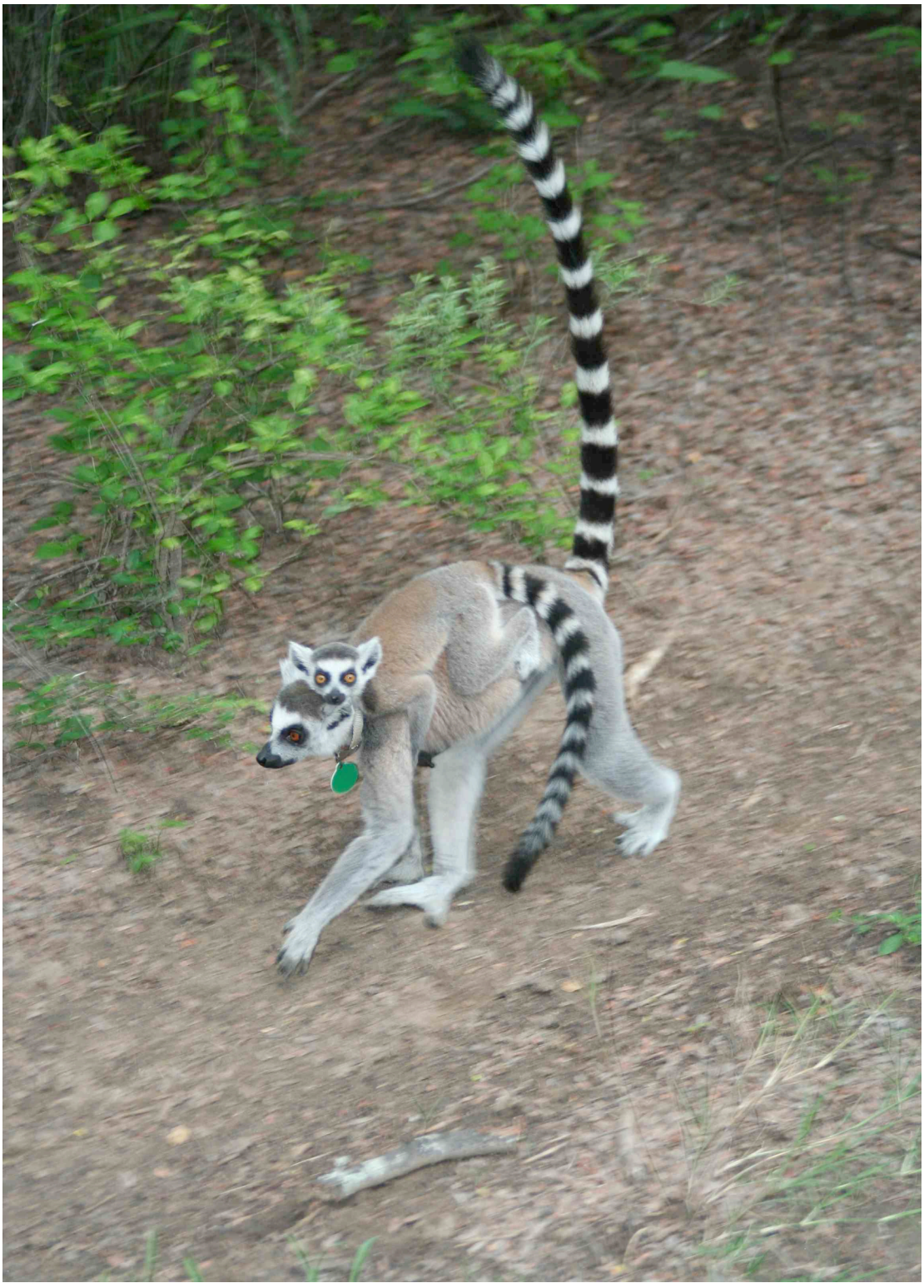

Figure 2.1c *Lemur catta* traveling terrestrially, mother and infant.

2.4 Preliminary Studies

During June–July 2001, Dr. Sauther and I conducted extensive fieldwork documenting habitat alteration in and around BMSR. We conducted habitat structure transects in both the protected intact Reserve of BMSR as well as the anthropogenically altered habitat around the Reserve. We also carried out a census for *L. catta* groups to determine the presence or absence of ring-tailed groups in different types of habitats (Whitelaw and Sauther 2002, 2003). Troops that will serve as focal groups for my proposed project were located. Skills that I have acquired from this field experience and resulting analysis included focal-animal sampling, surveying and censusing lemurs, lemur identification, and measuring habitat variation via habitat transects. Most important, this work allowed me to locate and confirmed that there are a sufficient number of study populations around the Reserve in fragmented habitats to serve as focal study groups for my dissertation research. I also participated in a habitat survey across much of this species' range in southwestern Madagascar. From the resulting data we know what habitat types *L. catta* occupies. Furthermore, we rigorously documented the types of anthropogenic change that are affecting the habitats around BMSR (Whitelaw et al. 2005). Additionally, I have been trained in ArcGIS data collection and analysis to spatially analyze the data.

2.5 Ecological and Activity Differences by Habitat

The wealth of different habitats and anthropogenic disturbances around the Reserve offered an excellent opportunity for examining how *L. catta* respond to their increasingly anthropogenically altered habitats (Figures 2.2-2.8). Prior work at BMSR provides the following background for the comparison between the Reserve and anthropogenically altered habitats. Within the Reserve, food diversity and food availability are high and fallback foods (food resources that are available during the dry season when few other foods are available) are used

primarily in the dry season (Sauther 1992, 1998, Sauther and Cuozzo 2009). For Reserve Groups, this is primarily the fruit of *Tamarindis indica*. Food diversity and food availability are highly seasonal, resulting in seasonal changes in feeding ecology (Sauther 1992, 1998). Habitats are intact, with many foraging substrates available, including continuous canopy, mid canopy and a rich herbaceous ground layer which is an important lemur food resource (Sauther, 1992, 1998). The dominant canopy trees are *T. indica*. Groups have core areas, which they defend from other groups (Sauther, 1999). Home ranges average 17 ha. in the Reserve but average 32 ha. in the drier vegetation-sparse western part of the Reserve (Sussman, 1991). In the anthropogenically altered habitats food diversity is reduced with fewer species available, and overall resources reduced. Fallback foods include *T. indica*, and also human crops, and an invasive species, *Argemone mexicana* (Whitelaw 2001, Whitelaw and Sauther, 2002, LaFleur and Gould, 2009). Both humans and their dogs often chase groups using human crops. Food diversity and food availability are also highly seasonal, resulting in seasonal changes in feeding ecology. Habitats here have been dramatically altered with many large canopy trees missing. Thus, mature canopy trees are widely spaced, there is little continuous canopy, few middle canopy trees and there is no herbaceous ground layer as heavy goat and sheep grazing has removed such herbs. The dominant canopy trees are also *T. indica* (Whitelaw et al., 2005). Groups have large home ranges with core areas, but there appears to be few areas of exclusive use, particularly during the dry season (Sauther, unpublished data). With regards to activity patterns, a preliminary comparison of the same troop's behaviors within the Reserve forest and anthropogenically altered habitats indicate that social behaviors are greater and that there is greater use of arboreal substrate within the Reserve (Sauther et al, 2006). Groups within the Reserve are highly synchronous in their behavior, e.g. they all tend to sleep, feed, forage and

travel together (Sauther, 1992). In anthropogenically altered habitats members spent more time moving overall and used terrestrial substrates more often. Feeding agonism was also much higher than when in the Reserve (Sauther et al., 2006). Preliminary data also suggest they are less synchronous in their behavior outside the Reserve (Sauther et al., 2006).

Figure 2.2 Anthropogenically disturbed agricultural area north of Parcel 1.

Figure 2.3 Anthropogenically disturbed agricultural area south of Parcel 1.

Figure 2.4 Anthropogenically disturbed area harvested for trees southeast of Parcel 1.

Figure 2.5 Anthropogenic disturbance between Sakamena River and gallery forest south of BMSR.

Figure 2.6 Eastern border of intact Parcel 1 along the Sakamena River.

Figure 2.7 *Lemur catta* feeding on terrestrial herbs in Parcel 1.

Figure 2.8 Gallery forest within Parcel 1 with marked trails.

2.6 Recent Research and Developments at BMSR

2.6.1 Current Research at BMSR

BMSR has been the site of active research in multiple areas of study since 1987. More recently, however, with several of the primary researchers' graduate students utilizing the site and primary researchers having active research teams, ring-tailed lemurs at BMSR have been the focus of biomedical, conservation, ecological, and behavioral ecological studies. For example, health and disease studies have shown that individuals living in marginal, unprotected, anthropogenically altered habitats tend to exhibit lower fat stores, tend to be less hydrated, and exhibit a higher frequency of severe tooth wear accompanied with antemortem tooth loss, (Junge and Sauther 2006, Miller et al. 2007, Sauther et al. 2006, Sauther and Cuozzo 2009). Furthermore, comprehensive research on dental data from more than 80 individuals has illustrated that ring-tailed lemurs at BMSR can sustain a high frequency of severe wear and antemortem tooth loss (Cuozzo and Sauther 2004, 2006; Sauther et al., 2002). This tooth loss is a function of severe and intensive wear, primarily due to focusing on kily (*Tamarindus indica*) fruit (Millette et al. 2009, Sauther and Cuozzo 2009).

Additionally, a recent nine-month study examining the interplay of habitat and parasite ecology revealed that ring-tailed lemurs harbor significantly more endo- and ectoparasites than sympatric sifaka (*Propithecus verrauxi*) (Loudon 2009). This result was strongly linked to higher rates of grooming behavior in ring-tailed lemurs, their semi-terrestrial traveling patterns, and more general, omnivorous dietary strategy. Furthermore, this study illustrated that ectoparasite intensity was linked to increased grooming rates in the dry season. Grooming rates proved to be a strong factor in predicting parasite loads: Groups that groomed more (groups in protected, Reserve habitats) harbored more ectoparasites (Loudon 2009).

Increasingly, researchers have been focusing on the differences between Reserve and Non-Reserve habitat ring-tailed lemur groups (Sauther and Cuozzo 2009, Millette 2009, Gemmill and Gould 2008, LaFleur and Gould 2009, Loudon 2009, Whitelaw 2001, Whitelaw and Sauther 2002, 2003; Whitelaw et al. 2005, 2007). This is symbolic of the shift from investigating lemurs in relatively intact habitats, to using the comparative method and examining ring-tailed lemurs in both intact and disturbed habitats. Results from these studies on biomedical, biological, demographic, behavioral, and ecological levels have been insightful and are contributing to the wider understanding of how primates negotiate, and adapt to, anthropogenic change.

2.6.2 Evaluating Stochastic Events at BMSR

Madagascar is known for its unpredictable environments, and is periodically affected by cyclones, drought, fire, and storms that can dramatically impact wildlife populations (Dewar and Richard 2007, Dunham et al. 2008, Ganzhorn 1995, Godfrey and Irwin 2007, Gould et al. 1999, Gould et al. 2003, Wright 1999, 2006, Ralainasolo et al. 2008, Rasamimanana et al. 2000, Ratsimbazafy 2006, Ratsisetraina 2007, Tarnaud and Simmen 2002). Moreover, these destructive storms may have played an important role in the evolutionary history of the flora and fauna of Madagascar (Binggeli 2003, Wright 1999). While these storms are an annual occurrence, very little is known about their effects on Malagasy ecosystems. Increasing examination of these stochastic events is showing that they can have profound effect on primate populations in Madagascar. For example, the passage of cyclone Gretelle in 1997 destroyed 75% of the trees in Manombo Forest in southeastern Madagascar and studies there indicate that this event severely restricted resource availability for lemurs in the area (Ralainasolo et al. 2008, Ratsimbazafy 2006). Further, this cyclone's direct hit caused surviving native trees a loss of

85% of their crown volume. Researchers believe that these effects reduced fruit production in the productive vegetation by more than 70% (Wright 1999, Ratsimbazafy 2006). Examining the impacts of catastrophic and stochastic events requires comparative evaluation of ecological patterns prior to the event and after the storm has occurred. These opportunities are rare, and this dissertation has the comparative advantage to look at historical phenological data and feeding information, and compare it to the data collected after Cyclone Ernest hit the southwestern region of Madagascar particularly intensely in January of 2005. Madagascar frequently experiences several cyclones per year. In fact, there were two strong cyclones in January and February of 2006 that disrupted this study. Unexpectedly, my dissertation work offers the opportunity to examine the impacts of habitat degradation due to both natural and anthropogenic causes.

In general, high wind velocity of cyclones and hurricanes can cause significant damage to forests (Everham and Brokaw 1996). Frequently, trees are uprooted and completely defoliated and deflowered (Dittus 1985a, Pavelka et al. 2003). Consequently, this induces significant damage to the food supply of both folivores and frugivores, not to mention damage to locomotor pathways and sleeping sites. A cyclone in Belize, for example, reduced howling monkey food resources by 35% (Pavelka and Behie 2005). Further, other studies have illustrated that natural disasters, such as cyclones, have significantly impacted the behavioral ecology of primates. For example, because the food supply is dramatically reduced and altered after a catastrophic storm, primates have been shown to modify their dietary strategy and select less preferred food choices, or have a less diverse diet following the impact (Berenstain 1986, Behie and Pavelka 2005, Tsuji and Takatsuki 2008). Compounding the effects of defoliation of a storm, defoliation can also

force folivores to feed on fallback foods not normally exploited. As a consequence, this overbrowsing can cause trees to die (Dittus 1985b).

Not only do these stochastic events affect feeding, they can alter activity budgets, increase group spread during foraging, and decrease travel time and daily path lengths (Berenstain 1986, Tsuji and Takatsuki 2008). Furthermore, modifications to the arboreal landscape and pathway system have been shown to disrupt arboreal travel for long-tailed macaques and forced them to spend more time traveling terrestrially (Berenstain 1986). Interestingly, cyclones can cause a significant amount of biomass to shift from the canopy to the forest floor, thereby increasing terrestrial travel because arboreal pathways are relocated (Lugo 2008). These changes can lead to increased vulnerability to both terrestrial and arboreal predators. Animal populations, including primates, have been shown to have increased mortality resulting from both direct and indirect effects on habitats resulting from cyclones (Lugo 2008).

In southeastern Madagascar, at Manombo, a comprehensive study of ruffed lemurs (*Varecia variegata*) documented the effects on this species' behavioral ecology three years after a severe cyclone hit in 1997 (Ratsimbazafy 2006). This study illustrated that while *V. variegata* appears to be an obligate frugivore, they also have the ability to adjust their feeding strategies. As there were fewer fruiting trees due to the severe cyclone damage, *Varecia* at this site spent significantly more time consuming fruit from shrubs and vines than at other sites. This research highlights the ability of primates to diversity their diets and use opportunistic strategies to use food species: *Varecia* at Manombo tended to travel less and forage solitarily. Further, these primates were able to focus on the fruit of exotic species, because endemic species were not as productive after the effects of cyclone Gretelle. These data suggest that primates may employ both behavioral and feeding strategies to cope with stochastic changes to their food supply.

The impact of Cyclone Ernest in the BMSR region included tree falls, massive defoliation and a widespread decrease in food availability for wildlife both inside and outside the Reserve (LaFleur and Gould 2009, Sauther, pers. obs.) (Figures 2.9, 2.10). Compounding the overall reduction in food availability, the fruit of *Tamarindus indica,* a noted fallback food for *L. catta* (Budnitz and Dainis 1975, Gould 2006, Jolly et al. 2002, Koyama et al. 2006, Mertl-Millhollen et al. 2003, Rasamimanana and Rafidinarivo 1993, Sauther 1992, 1998, Sauther and Cuozzo 2009, Simmen et al. 2006, Yamashita 2002), was dramatically reduced in availability due to the cyclone's effect on stripping a majority of the trees of their flowers in January of 2005 (Youssouf, unpublished data). This study began in September of 2005 and records the phenological and ecological aftermath of this particularly devastating cyclone. All phenological and demographic results collected during this study period must be examined in light of Cyclone Ernest since its impact may have affected infant survival, pregnant females' feeding opportunities from May – October, and feeding ecology for the entire BMSR population. Lemur conservation strategies, in general, must include stochastic and devastating cyclone activity into account because the effects can be catastrophic. Ecosystems can have biotic responses ranging from the immediate (within seconds), to the long-term (centuries) (Lugo 2008). In the past decade, significant discussion has been devoted to how stochastic events, such as cyclones, compound the anthropogenic disturbance to create an increasingly unpredictable, challenging, and complex ecological landscape (Dewar and Richard 2007, Dunham et al. 2008, Ganzhorn 1995, Godfrey and Irwin 2007, Gould et al. 1999, Gould et al. 2003, Rasamimanana et al. 2000, , Ratsimbazafy 2006, Ratsisetraina 2007, Ralainasolo et al. 2008, Tarnaud and Simmen 2002, Wright 1999, 2006).

Figure 2.9 Downfall from Cyclone Ernest in Parcel 1 of Beza Mahafaly Special Reserve.

Figure 2.10 Downfall from Cyclone Ernest in Parcel 1 of BMSR.

This study complements these biological studies with a comprehensive examination of the phenology, behavior, birth season patterns and habitat differences after a destructive cyclone year. While much of the data must be qualified with the effects of the January 2005 cyclone, this study is powerful in that it provides the first comprehensive, cross-season examination of these variables since Dr. Sauther's research in 1987-88 and allows us to compare patterns in a normal and post-cyclone year.

2.7 Study Site

2.7.1 History of Beza Mahafaly

Beza Mahafaly Special Reserve is located approximately 35 kilometers southwest of Betioky-Sud, situated next to the Sakamena river at 44°32'20" latitude south and 44°34'20" longitude east (Figure 2.11). The Sakamena is a tributary of the much larger Onilahy river, approximately 10 kilometers to the north. This Reserve was officially inaugurated in June of

1986 as a result of local, national, and international partners designating this forest a center for research, education, development projects, and conservation partnership (Sussman and Ratsirarson 2006). Since its inception, the Reserve has hosted a multitude of researchers, graduate students, and Malagasy university students to learn about the wealth of biodiversity, conservation measures, and contribute to the growing knowledge of this important protected area. After passing through the operative hands of the World Wildlife Fund and the Department of Water and Forests of the School of Agronomic Sciences (Ecole Supérieure des Sciences Agronomiques, Départment des Eaux et Forêts; ESSA/Forêts), the Reserve is now overseen by MNP (Madagascar National Parks the National Agency to manage the network of protected areas in Madagascar), and the University of Antananarivo through ESSA/Forêts. A permanent Malagasy staff remains at the Reserve year-round to oversee ecological monitoring and ongoing research projects.

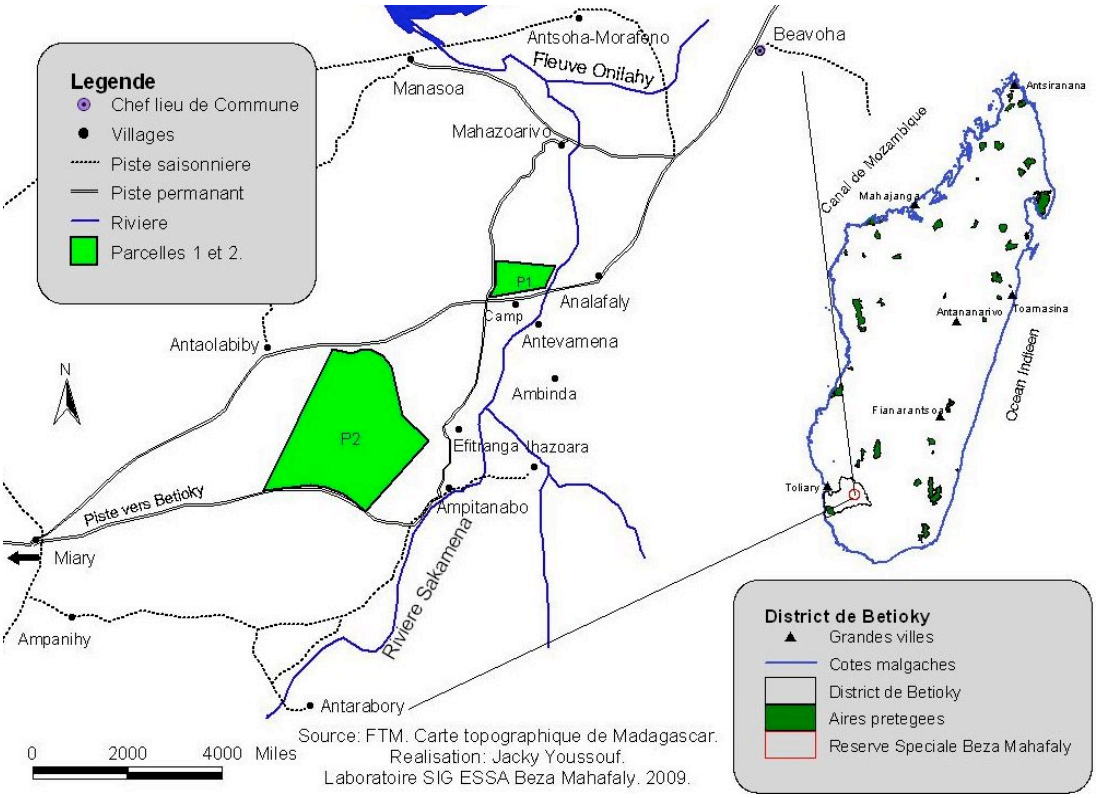

Figure 2.11 Map of Beza Mahafaly Special Reserve and surrounding region. P1 and P2 refer to the two Non-contiguous parcels comprising the protected area of this Reserve. Solid black circles indicate locations of local villages located within a 7 km radius of BMSR; black lines indicate road locations. From Youssouf, 2009, with the author's permission.

2.7.2 Biodiversity of Beza Mahafaly

Biological studies in the region have indicated a high level of biodiversity and richness of life in this area of southwestern Madagascar (Sussman and Rakotozafy 1994, Sussman and Ratsirarson 2006, Ratsirarson et al. 2001, Ratsirarson 2003). There are four species of lemurs, two nocturnal and two diurnal. Diurnal species are, *Lemur catta,* the ring-tailed lemur, and *Propithecus verreauxi*, Verreaux's sifaka. The nocturnal species are *Lepilemur leucopus*, the white-footed lepilemur, and *Microcebus griseorufus*, the gray and red mouse lemur. One recent study has indicated that although mouse lemurs tend to vary individually in pelage color in the Reserve, they all belong to the *M. griseorufus* clade (Heckman et al. 2006). Other mammals include four species of bats; four species of tenrec; and two endemic rodents (*Eliurus myoxinus*

and *Macrotarsomys bastardi*) and two introduced species (*Rattus rattus* and *Mus musculus*) (Youssouf and Rasoazanabary 2008), and; three species of carnivore (two of which are introduced). The nocturnal wild boar has not been seen here for many years (Ratsirarson 2003).

Other animal species demonstrate the richness of this Reserve by the number of family level groups represented. These include a highly diverse array of bird life: 102 species identified, five of these are endemic to southern Madagascar and more than half of the families consist of only one species (Ratsirarson et al. 2001, Sussman and Ratsirarson 2006). In addition to the avifauna, BMSR is home to at least 15 species of snakes, 18 species of lizards, two species of tortoise (one being the critically endangered radiated tortoise, *Geochelone radiata*), one species of freshwater turtle, and one seasonally present species of crocodile. There are three species of amphibians in the Reserve as well. Of the reptiles, the geckos are particularly diverse, consisting of six genera (Sussman and Ratsirarson 2006). In addition to the bird, reptile, and amphibian life, BMSR is host to a diverse array of insects. These include 105 species of moths and butterflies of 16 families; 46 species of beetles of 17 families; and 28 species of ants, bees, and wasps (Ratsirarson 2003).

The biodiversity of the flora of Beza Mahafaly has been well studied and is marked by not only dry-adapted species, but by a majority of endemic (to southwestern Madagascar) species, with the exception of anthropogenically disturbed areas (Sussman and Ratsirarson 2006, Ratsirarson 2003, Ratsirarson et al. 2001, Sussman and Rakotozafy 1994). Moreover, Beza Mahafaly is recognized as the only protected area in Madagascar exhibiting a xeric gradient moving from gallery habitat to spiny (xeriphytic) forest (Ratsirarson 2003). This provides another level of depth and complexity to studies in this area as the floral composition is not an independent variable, but a dynamic force in determining some faunal distributions (Sussman

and Rakotozafy 1994). These include several deciduous species, species with spines, species without leaves or with small succulent leaves, and species with tubers (Ratsirarson 2003). In sum, these forests contain approximately 112 species from 49 families (Sussman and Ratsirarson 2006). While gallery forests near the Sakamena River are dominated by deciduous and semi deciduous trees such as *Tamarindus indica, Albizia polyphylla, and Acacia rovumae,* forests occurring at increasing distances from the river are dominated by *Euphorbia* spp., *Cedrelopsis grevei*, and *Alluaudia procera* (Ratsirarson 2003). Several researchers have noted that with the gradual change in flora from east to west, moving west from the river, there are changes in the density and distribution of at least one lemur species, namely *Lemur catta* (Sussman 1991, 1992; Whitelaw and Sauther 2003).

2.7.3 Climate

Climatically, semi-arid southern Madagascar is well known for its long dry season during the austral winter (April through October) and the hot wet season of November – March. The Sakamena River is typically dry through the winter. Average annual rainfall is approximately 750 mm; 600 mm of rain typically falls during the austral summer. The Sakamena normally floods periodically during the rainy season and can inundate surrounding fields and forests during particularly intense storms and cyclones (Ratsirarson 2003). These summer months also offer higher temperatures, averaging 34° C and ranging to 48° C. The cooler and drier season temperatures usually range from 23° C to 30° C, but can drop to 3° C during the nights of the coolest months in July and August.

Soils in this area are characterized by a sedimentary zone with a smaller limestone layer that is marked by karstitic processes (Ratsirarson 2003). Due to the strong influence of the rivers in this region, in general there are two markedly different types of soils. Gallery forests (such as

Parcel 1) and areas near the Sakamena River are characterized by alluvial soils. As the drier, and increasingly higher plateaus extend away from the river (such as Parcel 2), tropical ferruginous soil predominates. Local villages take advantage of the richer alluvial soils and concentrate their agricultural practices close to the Sakamena.

For this study, rainfall and daily temperatures were collected in the BMSR camp using an All-Weather Rain Gauge, made to US Weather Bureau specifications and using Taylor model 1441 Thermometer/Logger, Digital Max/Min. The digital thermometer recorded the highest and lowest temperature during a 24-hour period. During the study period, this research benefited from a partnership with the GLOBE program (Global Learning and Observations to Benefit the Environment) of the US Government, based at the National Center for Atmospheric Reserarch (NCAR) in Boulder, Colorado with NCAR. My husband, Jason Albert (a Boulder Valley School District teacher) brought local teachers from around BMSR to learn basic climate and weather data collection to begin a mosquito and malaria research program for the GLOBE program. Consequently, we used the GLOBE program's standard weather and climate research station equipment to acquire both rain and temperature data for the study period. From October 2005 through July 2006, the total number of days that precipitation was collected was 53.

In contrast to previously published precipitation numbers, I recorded a total of 385.4 mm of rain from November 2005-June 2006 (Figure 2.12). Previous accounts have been closer to 600mm (Sussman and Ratsirarson 2006, Sauther 1993, Sussman 1991). This may be due to incorrect rain collection data during several severe cyclones in January and February of 2006 that overflowed the rain gauge. In terms of temperature during the study period, the mean temperature for the austral summer (November to March) was 37.3°C (range 11.7° - 43.7°C). In

contrast, the mean temperature for the austral winter (April to October) was 31.6°C (range 7.2°-41.0°C).

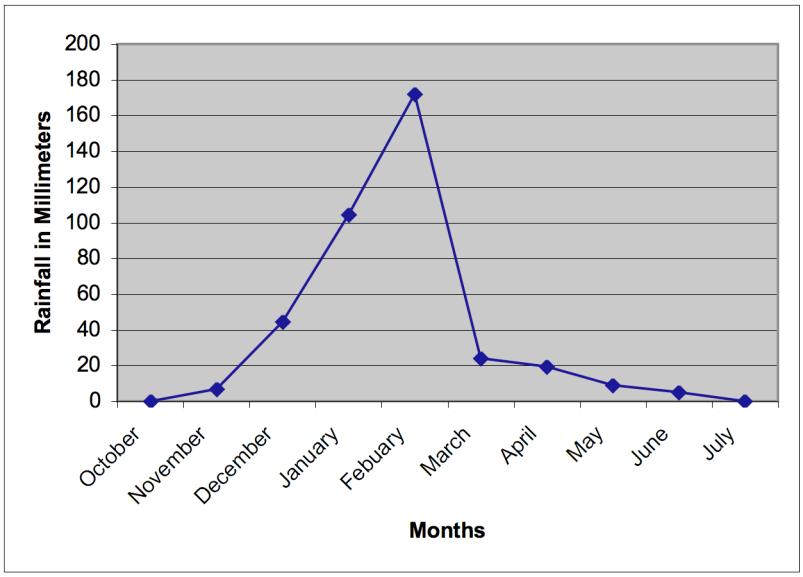

Figure 2.12 Rainfall at Beza Mahfaly Special Reserve from October 2005 – July 2006.

During my study, from September 2005 – June 2006, Beza Mahafaly Special Reserve (BMSR) consisted of two Noncontiguous parcels separated by approximately 10 kilometers. From the landscape view, Parcel 1 sits on the banks of the Sakamena River and is dominated by gallery forest and *Tamarindus indica* in the east giving way to the drier, xeriphytic forests to its western boundary farther from the higher water table of the river. It consists of 80 hectares, systematically divided by trails into 100m x 100m squares. This parcel has been fenced by barbed wire since 1979 and has an extensive trail system, which divides the parcel into 1 ha^2 quadrants (Sussman and Ratsirarson 2006, Sussman and Rakotozafy 1994). Before this time, grazing by cows and goats and selective harvesting of trees for firewood and housing was frequent (Sussman and Ratsirarson 2006). Presently, these activities are common just outside the borders of the Reserve (Sussman and Ratsirarson 2006, Whitelaw and Sauther 2002). The

forested land west of the Sakamena lies flat, at an elevation of approximately 100-200 meters above sea level. The Reserve is relatively flat with successively rising plateaus beginning at the Sakamena (Ratsirarson 2003). Surrounding Parcel 1 is unprotected, increasingly degraded gallery forest to the north and south, and fairly contiguous xeriphytic forest to the west (increasingly distant from the higher water table supplied by the seasonal river). The southern and western end of the 80 hectare Parcel 1 are bounded by dirt roads that lead to local villages.

The second, Non-contiguous parcel, Parcel 2, consists of approximately 520 hectares of predominately xerophytic forest (Sussman and Ratsirarson 2006). Often referred to as the spiny forest, it is dominated by plants of the endemic family of Didieriaceae. Unlike Parcel 1, Parcel 2 has been the focus of study for only a handful of research projects. This is partially due to its location farther from the research support center adjacent to Parcel 1. Consequently, there are very few collared lemurs in Parcel 2 for long-term, individual focused projects. Under agreements with local officials and MNP, BMSR has recently been expanded to approximately 3000 hectares. This extension will not be fenced, like Parcel 1, but will connect the two parcels.

BMSR has an extensive research camp south of Parcel 1 across a simple dirt road (leading to Analafaly). Situated beyond a gate and fence, BMSR camp consists of a concrete office building and museum, two wooden houses, an outdoor cooking area with concrete work areas, an open gazebo structure with a concrete floor featuring tables, two concrete outhouses, a concrete showerhouse, and a camping area sheltered by Tamarind trees suitable for researchers' tents. These structures host researchers, the occasional tourist, and local meetings concerning the Reserve and local villages.

There are local villages that are situated in the landscape of the Beza Mahafaly Reserve. Villagers utilize the landscape for agriculture (cassava, rice, corn, beans, onions, tomatoes),

grazing herds of cattle, goat, and sheep, and selective tree harvesting for cooking and building shelter. The richest agricultural plots are located in the alluvial soils near the Sakamena River (Ratsirarson 2003). Local farmers use crop rotation and let fields fallow for several years at a time. The closest villages are Antavamena to the southeast (approx. 1 km), Analafaly to the east (approx. 2 km) and Mahazoariva to the north (approx. 4 km). Members of the permanent BMSR staff reside in these nearby villages. In addition, national and international researchers at BMSR typically hire research assistance from individuals in these local villages with knowledge of local biodiversity, and individuals who can provide cooking and laundry services and supplies (produce, meat, eggs) from nearby sources.

2.8 Data Collection

2.8.1 Data Collection: Forest Structure

Across a five-day period in April and June, 2006, James Loudon and I quantified habitats on five, 300 meter long transects using the point-centered quarter method inside BMSR and south of the Reserve in unprotected, lemur occupied habitats. We collected data at 25-meter increments along the 300-meter transects resulting in 12 data points for each transect (Dahdouh-Guebas and Koedam 2006). Two of the transects were located inside Parcel 1 and three were located in the home ranges of two *Lemur catta* groups residing primarily to the south of BMSR in unprotected areas. These habitats' data will be described below as Reserve habitat 1 (Teal Group's range), Reserve habitat 2 (Green Group's range), Non-Reserve habitat 1 (Black Group's range and encompassing part of the research camp), Non-Reserve habitat 2 (Light Blue Group's range), and Non-Reserve habitat 3 (in between Black and Light Blue Group ranges, but primarily Black Group's range) (Figure 2.13). I chose this method because it demonstrates the least variable results, provides more sampling per point, and is the least susceptible for bias

(Dahdouh-Guebas and Koedam 2006, Brokaw and Thompson 2000). In this study, all point transects overlay home ranges of the project's *Lemur catta* study groups. I did not place these transects completely randomly inside the home ranges of my four study groups as I wanted to avoid sampling areas that were infrequently used by my study subjects and/or altered by local human made trails and roads. Instead, transects were chosen to cover evenly home ranges utilized by *L. catta* and avoided maintained human trails. That being said, I did use a random segment transect generator to acquire a random shape to the 300 meter point transects. This process generates a shapefile of randomly placed transects (both position and angle) within the selected polygon features (the home range shape). I supplied inputs including whether or not the transects can overlap, the sampling width, minimum and maximum transect lengths and specified a number of segments within the polygon. These transects were divided into 100 meter segments that changed in a random direction at each 100 meter segment. Not only did this supply me with a random transect shape and data collection tool, it also covered the polygon home range shape more comprehensively than a simple, straight 300 meter segment. Specifically, the transect maintained the same compass direction for the first 100 meters, changed direction for the second 100 meter segment and changed direction a second time for the final 100 meters (see Figure 2.14).

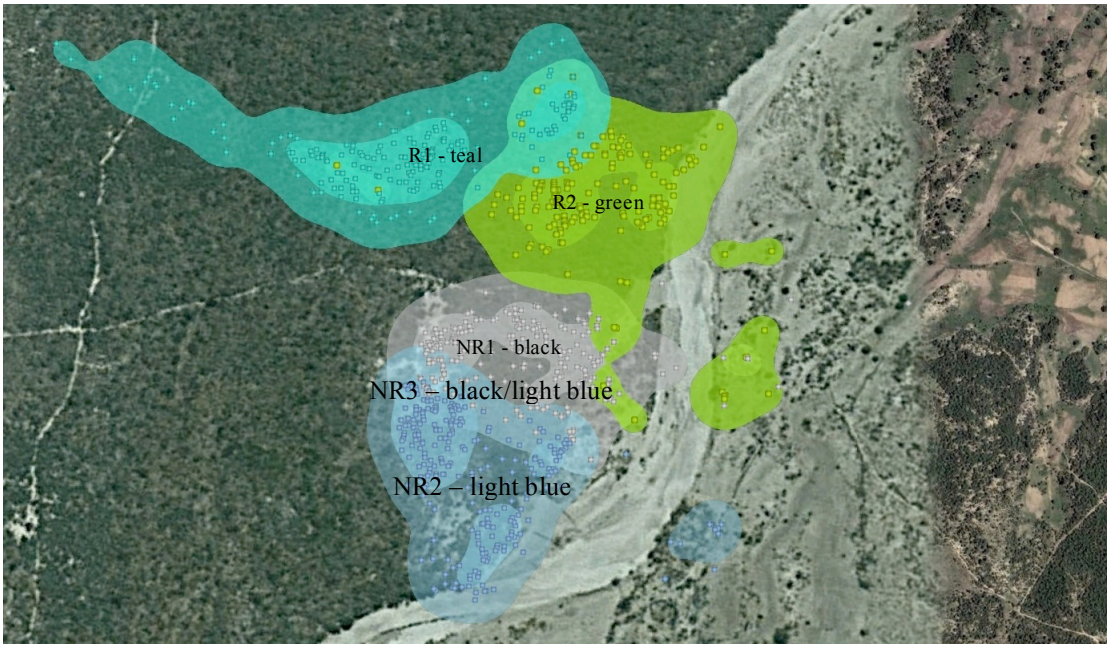

Figure 2.13 Map depicting Teal (Reserve 1 – R1), Green (Reserve 2 – R2), Black (Non-Reserve 1 – NR1), and Light Blue (Non-Reserve 2– NR2) Groups' home ranges.

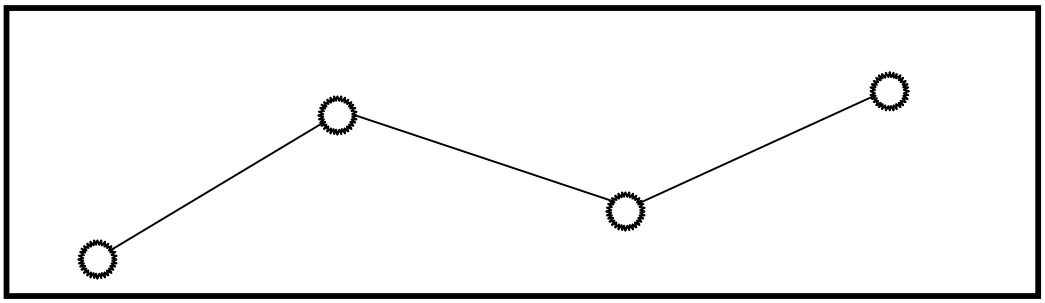

Figure 2.14 Example of random point transect generated. Each segment is 100 meters long.

Along each transect, we collected biological information for trees in each quarter of the transect point, closest to the transect sampling point, ≥ 5 cm diameter at breast height (DBH) (see Figure 2.15). These data include: distance to focal point (*a* in Figure 2.15); DBH; tree species (species identification was supplied by a permanent member of the ecological monitoring team, Elahavelo); height; average crown diameter (calculated by taking the average of two, perpendicular diameters); incidence of lianas (vines); canopy connectedness; distance to nearest

sapling; sapling species; distance to nearest shrub; shrub species; number of valiandro (*Quivisianthe papinae*), kily (*Tamarindus indica*), and filo filo (*Azima tetracantha*) saplings (selected due to their contribution to both *Lemur catta* feeding ecology and importance in forest structure); number of herbs present in two 1m x 1m plots placed randomly alongside the transect line; presence of agricultural fields within 30 meters; presence of a human path or road within 30 meters; evidence of tree harvesting within 15 meters; presence of zebu (cattle) feces within 15 meters; soil compaction measurement; light meter reading. Soil compaction measurements (taken with a soil penetrometer: Cole Palmer WU-99039-00) are a quantification of the amount of traffic (from human foot traffic, livestock, or wildlife). Light meter readings (taken with a light meter from: EXTECH instruments, model #401025) offer a further quantification of the amount of light reaching the forest floor (a lower reading indicates less light reaches the forest floor while higher light readings indicate a greater disconnect in the canopy).

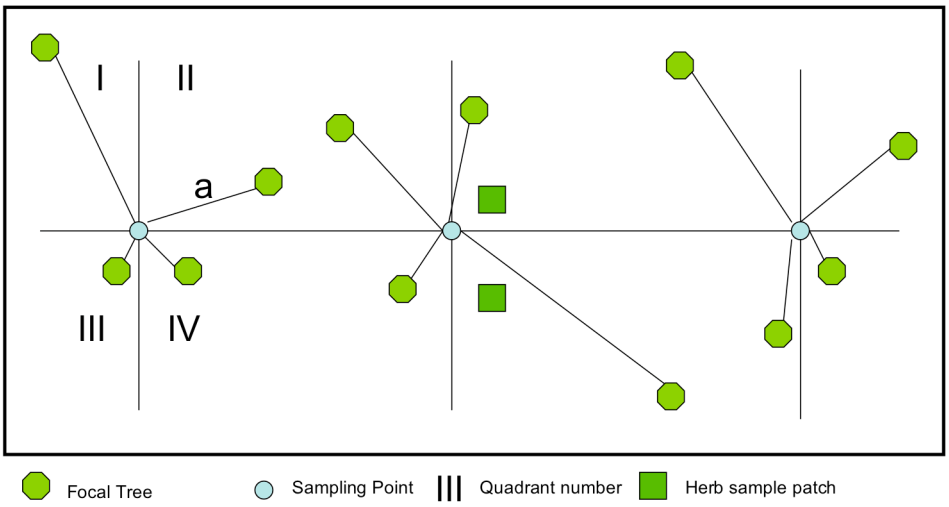

Figure 2.15 Diagram of Point Centered Quarter Method.

2.8.2 Data Collection: Phenology

During the course of the study, I monitored 90 plants between October 2005 and June 2006. I used the "selected tree" method (Hemingway and Overdorf 1999). This method strives for unbiased results by identifying and tagging targeted trees that represent common tree species in the forests (based on species listed in Ratsirarson et al. 2001) in addition to common food sources of the ring-tailed lemur, *L. catta* (70% of trees were *L. catta* food trees). Thirty of the trees were inside the Reserve, situated along a trail that began in the western, drier part of the protected area (Figure 2.16). The remaining 60 were situated south of BMSR in the home ranges of the two lemur groups residing in unprotected areas (Figure 2.17). Additionally, these trees were all of similar DBH, large, and mature trees.

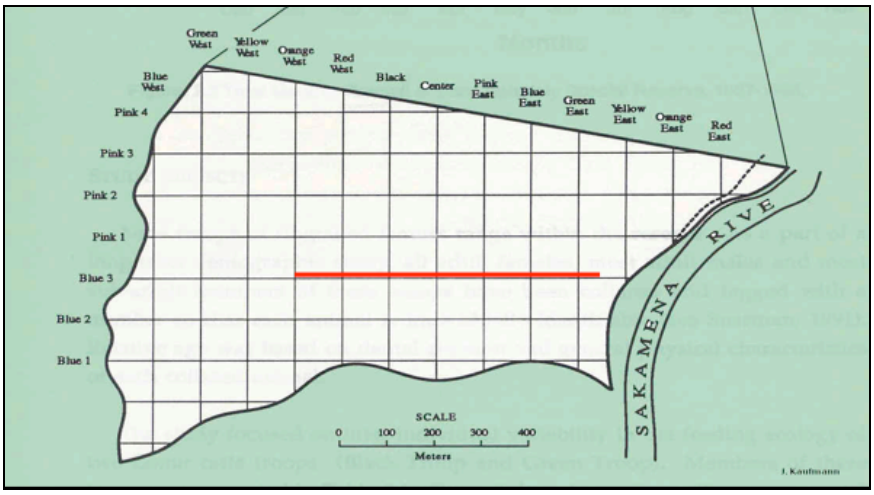

Figure 2.16 Map indicating Parcel 1 phenology transect.

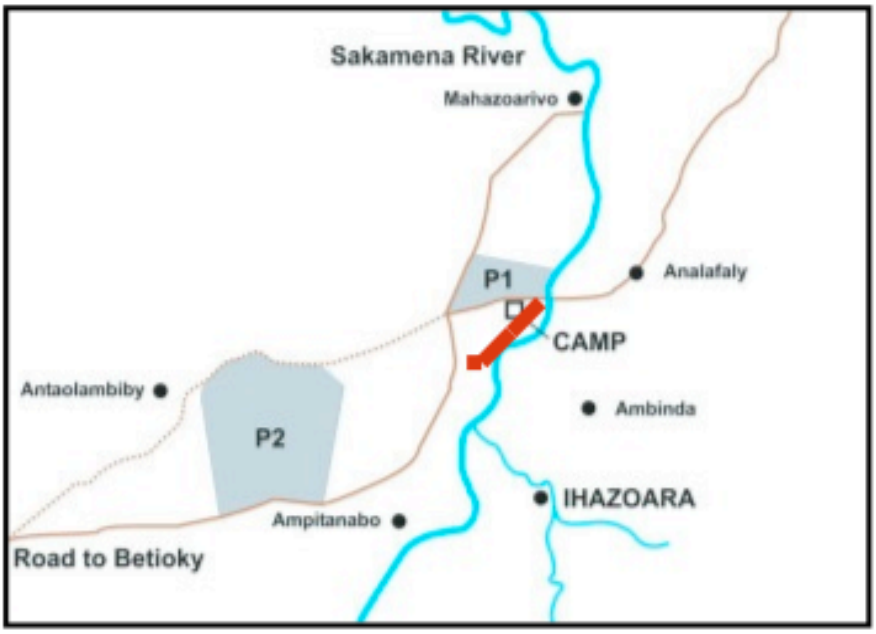

Figure 2.17 Red line indicates location of phenology transect in anthropogenically disturbed, unprotected *Lemur catta* habitats outside of Parcel 1.

All plants were monitored twice a month, approximately two weeks apart. Typically, phenological data are collected monthly, however, feeding ecology patterns among *L. catta* change rapidly and I attempted to capture changes in their behavior with changes in food availability. I collected phenological data at the beginning of each month, and approximately

two weeks later. Finally, I monitored each transect on the same day to eliminate bias based on timing.

Each tree was assigned a score based on the stage of its leaves, flowers and fruits. BMSR ecological monitoring team member, Elahavelo, walked each transect with me and assisted with the scoring system as it is identical to the system used for their regular monitoring research (Table 2.1). To avoid the problem of presence-absence methodology and scoring trees with only one or two flowers or fruits with a higher score, the score was given for the most abundant phenological phase present. Only when phenological phases were present in the same quantity, was a combined score given to a particular tree. Scores were then added to produce a total phenological abundance score for the month for each phase. For example, if 10 trees had ripe fruit in the Reserve habitat, then the total abundance score for that month would equal 20 (see figures 3.14 and 3.15 for results). The higher the phenological score (on the Y-axis in chapter 3 figures 3.14, 3.15, 3.16, 3.17), the more abundant this particular resource (fruit, leaf, flower) was during that month. This provides a general perspective on the abundance of each phenological phase to compare between habitats.

Table 2.1 Phenological scoring information

Phenological Score	Phenological Score Description
0	No fruit, flower, leaf present
1	Leaf buds (Young leaves) or flower buds present
2	Developed, mature flowers, leaves or ripe fruit present
3	Very mature or dry leaves, flowers, or fruit present

2.8.3 Data Collection: Study Groups

To conduct a comprehensive comparative study between ring-tailed lemurs living in a relatively undisturbed habitat with those inhabiting anthropogenically altered and disturbed areas, I examined four groups: two residing in Parcel 1 of BMSR and two inhabiting disturbed habitats south of the Reserve in gallery forest adjacent to the Sakamena river. This approach allows comparisons between conspecifics in similar habitats in that they are dominated by gallery forests and *Tamarindus indica* groves, but inherently affected by anthropogenic activities, or lack thereof. The two study groups within the Reserve will be referred to as "Reserve Groups" at BMSR (inside the fenced and monitored Parcel 1) while the two study groups outside the BMSR Parcel 1 will be referred to as "Non-Reserve Groups".

The *L. catta* population in and around BMSR has been part of long-term biological, ecological, demographic, and behavioral studies (e.g., Cuozzo and Sauther 2004, 2006; Gould et al. 2003; Gould and Sauther 2006; Junge and Sauther 2006; Sauther 1992; Sauther et al. 1999, 2001, 2002; Sauther and Cuozzo 2008). As such, the majority of adult ring-tailed lemurs, unless they were a very recent immigrant, are collared with different colored collars fastened with nylon thread and holding a single plastic numbered tag. Each group (Green, Red, Teal, etc.) is fitted with the same color collar and the numbered tag is the distinguishing feature among them. From the onset of the study, individuals could be reliably identified even if there was a recent immigrant male as no group had more than one uncollared individual per age/class size (adult, subadult (age 2-3 years), juvenile (age 1-2 years), infant (0-1 year)).

Ring-tailed lemur behavior has been well studied and groups are characterized by multi-male, multi-female, female-bonded societies in which females usually remain in their natal

groups (Gould 2006; Jolly 1966; Sauther, 1992; Sauther et al. 1999; Sussman 1992). Adult females are dominant and receive priority access to all resources (Jolly 1966, 1984; Sauther 1993, Sauther et al. 1999) A typical group consists of a several related adult females and their offspring (usually juveniles and infants), one or a few central males (central males tend to be the alpha male of the group and have the closest proximity to females and preferred resource use), and a few more peripheral males. Males will disperse several times during their lives. Some groups may have more than one matriline, and in these cases one will be more dominant (Nakamichi and Koyama, 1997; Sauther 1992; Taylor and Sussman 1985, Jolly 1966). Groups sometimes contain as many as 30 individuals at BMSR, however average group size is 11.5 individuals (Sauther, unpublished data).

For this study, I began observing the four study groups in September of 2005. For four weeks I habituated the groups to my presence, began learning their ranging patterns and could predictably locate them each morning for the majority of mornings. By the end of this period, I could reliably observe all groups at close distances without the lemurs exhibiting alarm responses including running away.

Green Group: Reserve Habitat

Within the Reserve, only four groups have been known to fission in a 20 year span of long-term studies (Gould 2006). During the 2005-2006 study period, one of these fissions occurred. In September of 2005, Green Group consisted of 14 individuals (Table 2.2). Soon after data collection began in October of 2005, three males emigrated (#7, and 2 uncollared males – Jack and Stripe). Male #7, also known as Popeye for his missing eye, was a natal male known to have lost his eye as an infant during an intertroop encounter (Gould, pers. comm.). While Stripe's situation is unknown after his disappearance in November of 2005, Popeye and

Jack attempted to emigrate to Red Group (residing in the Reserve, just to the south of Green Group's range), however only Jack was successful in joining Red Group. Popeye remained solitary, ranging between Green and Red troop's range for the duration of the 2005-2006 study period. These individuals are not included in the data analysis. Importantly, this group had two matrilines: one containing females 34, 459 and the other containing females 23 and 9. In late December of 2005, after considerable high levels of aggression from females 23 and 9 directed at 34 and 459, the latter females left with an uncollared female juvenile – presumably 459's daughter (LJ), because 34 has no nipples (confirmed by a veterinarian – Sauther pers. comm..). These three females, later joined in April of 2006 by male 182 from another Reserve Group (Teal) formed their own small group, Trois Fromage. These individuals (34, 459, LJ, and 182) will not be included in the analyses as the group proved very difficult to locate after their fission and I collected very little data on their behavior after this incident. A dominance hierarchy was established based on affiliative, aggressive, and spatial behaviors between individuals. The following table details members of Green Group and the description of their presence or absence from data analysis:

Table 2.2 Green Group, Trois Fromage, and Green Group Emigrants. Gray and yellow indicates individuals *not* included in analyses.

Individual	Sex	Age Class	Rank	Habitat Status	Comments
9	Female	Adult	1	Reserve	Infant *born*
23	Female	Adult	2	Reserve	Infant *died*
167	Female	Adult	3.5	Reserve	Infant *died*
235	Female	Adult	3.5	Reserve	No infant
175	Male	Adult	6	Reserve	
209	Male	Adult	7	Reserve	
BJ	Male	Juvenile	5	Reserve	Natal Juvenile

LJ	Female	Juvenile	3	Reserve	*Trois Fromage*
34	Female	Adult	1	Reserve	*Trois Fromage*
459	Female	Adult	2	Reserve	*Trois Fromage*
Popeye 7	Male	Adult	N/A	Reserve	Emigrated
Jack	Male	Adult	N/A	Reserve	Emigrated
Stripe	Male	Adult	N/A	Reserve	Emigrated
37	Male	Adult	N/A	Reserve	*Presumed dead*

Teal Group: Reserve Habitat

In September of 2005, at the beginning of the habituation period and data collection, Teal Group consisted of 12 individuals. Over the course of the study, group size dropped to five. Three males emigrated and attempted to join other groups, I continued to collect data on them since they remained within Teal's home range and habitat parameters as they shadowed other Groups. One male (#151) emigrated to Yellow Group in November and was not included in the analyses due to his early departure during the study period. Additionally, the only juvenile (TJ – Teal Juvenile) was last seen on November 5, 2005, and an adult female was presumed dead on December 31, 2005, after she was not located for two weeks. 182, 204, 219, and 230 all attempted to emigrate to other groups, but remained within Teal's home range and are included in the data analyses as I was able to collect sufficient data on these individuals. The table below details the individuals and their status during the 2005-2006 study period:

Table 2.3 Teal Group Individuals. Individuals in Gray were not included in analyses

Individual	Sex	Age Class	Rank	Habitat Status	Comments
144	Female	Adult	1	Reserve	Her infant died
162	Female	Adult	2	Reserve	No Infant

202	Female	Adult	3	Reserve	No Infant
134	Male	Adult	4	Reserve	Central Male
208	Male	Adult	5	Reserve	
219	Male	Adult	6	Reserve	Attempts to emigrate, but returns to Teal
204	Male	Adult	3	Reserve	Emigrates to Yellow Group
230	Male	Adult	1	Reserve	Emigrates to Yellow Group
182	Male	Adult	2	Reserve	Emigrates to Trois Fromage
151	Male	Adult	N/A	Reserve	Emigrated to Yellow Group
148	Male	Adult	N/A	Reserve	Presumed dead 12/31/05
TJ	Male	Adult	N/A	Reserve	Presumed dead 11/5/05

Black Group: Non-Reserve Habitat

At the onset of the habituation period during September of 2005, Black Group contained 11 individuals (Table 2.4). As data collection began in October, 2005, two individuals (Male 119 and Female 121) were presumed dead or emigrated. Additionally, 112 died in January, 2006 from a dog attack according to a member of the BMSR Ecological Monitoring Team. Data from these individuals were not included in analyses. Male 113 emigrated from Black Group in January of 2006, successfully joining Orange Group immediately; data on him are included. A natal male, Wyatt, presumably 110, 112, or 116's offspring was an uncollared subadult, subsequently collared Black 223 in June of 2006. Notably, Black Group is the only group in this study that regularly utilizes the research camp – an anthropogenically altered area with access to buckets of water and human food. The chart below details the individuals and their status during the 2005-2006 study period:

Table 2.4 Black Group Individuals. Individuals in Gray were not included in analyses.

Individual	Sex	Age Class	Rank	Habitat Status	Comments
110	Female	Adult	1	Non - Reserve	Infant *died*
116	Female	Adult	2	Non - Reserve	Infant
212	Male	Adult	3	Non - Reserve	
6	Male	Adult	4	Non - Reserve	
206	Male	Adult	5	Non - Reserve	
226	Male	Adult	6	Non - Reserve	
Wyatt (223)	Male	Subadult	7	Non - Reserve	Natal Male
113	Male	Adult	N/A	Non - Reserve	Emigrates to *Orange Group*
112	Female	Adult	N/A	Non - Reserve	*Presumed dead 1/2006*
119	Male	Adult	N/A	Non - Reserve	Presumed dead 10/2005
121	Female	Adult	N/A	Non - Reserve	Presumed dead 10/2005

Light Blue Group: Non-Reserve Habitat

Consisting of 15 individuals at the onset of the habituation period in September of 2005, Light Blue Group was the largest in this comparative study (Table 2.5). There were two uncollared males, presumed emigrants from southern groups; one of these disappeared in November of 2005 and was not included in the data. Furthermore, one female (128) and her infant, and male 236 disappeared in November of 2005 and were consequently not included in the analyses. There were no further immigrations or emigrations during the study period. The chart below details the individuals and their status during the 2005-2006 study period:

Table 2.5 Light Blue Group individuals. Grey rows indicate individuals not used in data analyses.

Individual	Sex	Age Class	Rank	Habitat Status	Comments
131	Female	Adult	1	Non - Reserve	No Infant
123	Female	Adult	2	Non - Reserve	No Infant
122	Female	Adult	3	Non - Reserve	Infant *died*
224	Male	Adult	4	Non - Reserve	
125	Male	Adult	5	Non - Reserve	
130	Male	Adult	6	Non - Reserve	
124	Male	Adult	7	Non - Reserve	
242	Male	Adult	8	Non - Reserve	
247	Male	Adult	9	Non - Reserve	
253	Male	Adult	10	Non - Reserve	
Clay	Male	Adult	11		
Duncan	Female	Juvenile	N/A	Non - Reserve	
128	Female	Adult	N/A	Non – Reserve	Presumed dead 11/25/2005 – Had infant
236	Male	Adult	N/A	Non - Reserve	Presumed dead or emigrated 12/2006
Uncollared	Male	Adult	N/A	Non - Reserve	

2.8.4 Data Collection: Behavioral

I collected behavioral data on the four study groups detailed above between October 2005 and June 2006. These months captured both the wet and dry seasons in the BMSR region. In general, I cycled through the Reserve and Non-Reserve Groups examining each Group for two days in the following repeating order: Green, Teal, Black, Light Blue. Groups proved difficult to locate, particularly those outside the Reserve and this method ensured that I could locate them early on the second day having noted their sleeping site the day before. Observations were made during day-long group follows and rotated through individual group members so as to equalize

sample size among individual lemurs and encompass almost 800 hours of contact time over 200 days. Habituation and distance estimation were secured during the September of 2005.

All behavioral data were collected on a hand-held, Palm LifeDrive © in Excel. I used the BMSR solar panels to recharge the LifeDrive © each afternoon, except when rainy season monsoons prevented the solar panels from being charged. I stored data on rewritable compact discs each week.

In the mornings, as often as possible, I located groups in the sleeping tree or as soon as they began moving. I used 10 - minute focal samples with a 1-minute interval to record behavior (Altmann 1974). For each minute I collected the following information: focal individual behavior, location and species of tree involved if individual was arboreal, plant part if feeding, arboreal height (0 if terrestrial), nearest neighbor distance, nearest neighbor location in tree, nearest neighbor height, nearest neighbor behavior. For each 10-minute sample, I also recorded all occurrences of aggression, inter-troop encounters, GPS location if any movement over 20m had occurred, general group behavior, group spread, group location in terms of terrestriality or arboreality, and canopy connectedness. Group spread was considered in the following manner: VC (individuals were sitting in contact or within 2m of each other); CL (individuals between 2-5m); MD (individuals were between 5-8m of each other); FA (individuals were between 8-15m of each other); and VF (several individuals were spread over 15m apart). I used a laser range finder to establish distances over 5m. Group behavioral data were recorded according to the majority of individuals' behavior, location, etc. For example, if half or more of the individuals were eating, I would record the group behavior as feeding. These data allow me to calculate group behaviors and compare between groups, sexes, Reserve vs. Non-Reserve using the number of intervals the particular behavior, food species, plant part occurred during data collection.

2.9 Hypotheses

My original study plan was to examine only the anthropogenic disturbance and its effects on the ecology of the BMSR ring-tailed lemur population. I intended to address the following hypotheses:

Q_1: How do anthropogenically disturbed habitats affect the ecology of *L. catta*?

Compared to Reserve Groups, L. catta in anthropogenically disturbed habitats will:
H_{1a}: Exhibit lower food diversity, with fallback foods providing an important resource throughout the year.
H_{1b}: Exhibit less seasonal changes in resource use.
H_{1c}: Utilize fewer substrates, primarily the tall canopy trees of *T. indica* and the terrestrial substrate where human crops are available.
H_{1d}: Have larger home ranges and few core areas of exclusive use.

Q_2: How do anthropogenically disturbed habitats affect the behavior of *L. catta*?

Compared to Reserve Groups, L. catta in anthropogenically disturbed habitats will:
H_{2a}: Spend more time feeding, foraging, moving and less time in social interactions in anthropogenically disturbed habitats.
H_{2b}: Exhibit higher frequencies of feeding agonism.

Q_3: How do anthropogenically disturbed habitats differ from Reserve habitats?

Compared to Reserve habitats, anthropogenically disturbed habitats will:
H_{3a}: Exhibit lower phenological scores for fruit, flowers, and young leaves.
H_{3b}: Exhibit fewer patches of terrestrial herbs.
H_{3c}: Exhibit more instances of anthropogenic disturbance (crops, grazing, tree cutting).
H_{3d}: Exhibit smaller crown diameters.
H_{3e}: Exhibit less diversity in species present.

2.10 Summary

Due to the catastrophic cyclone Ernest earlier in the year, this study has been expanded to not only examining the anthropogenic disturbance present in this BMSR region, but to also include the post-cyclone effects. Examining the compounding natural and anthropogenic disturbance provides a realistic and comprehensive assessment of Madagascar's two most potent habitat disturbance variables (Wright 1999). The following chapters will detail the background

and results for each topic discussed: habitat structure, feeding ecology, spatial ecology, activity budget, behavior, and demography.

CHAPTER 3

EFFECTS OF ANTHROPOGENIC DISTURBANCE ON THE FOREST STRUCTURE AND PHENOLOGY IN AND AROUND BEZA-MAHAFALY SPECIAL RESERVE, MADAGASCAR

3.1 Introduction

Disturbed forests can be described both qualitatively and quantitatively. Qualitative differences between continuous, protected, and/or undisturbed forests are readily visible at the landscape level. Fragments of former forests often consist of both reduced area and increased isolation from other forest habitats. Not only are these "larger picture" components affecting forest habitats in disturbed landscapes, but the smaller scale biotic and abiotic changes in forest habitats affect the structure, botanical species diversity, and phenological in disturbed forests (Irwin 2006, Lawes et al. 2000, Laurance 1994, Laurance and Bierregaard 1997).

Disturbed forests suffer from a long list of biologically detrimental effects. Research from both natural and anthropogenic events and processes, has shown that trees on the edges of disturbed areas and where continuous forests meet the matrix have higher rates of mortality and injury (Laurance et al. 1998). Humans have increased access to these areas and they also tend to be drier, have higher UV exposure, and are more susceptible to wind damage. These effects can sometimes be seen up to 300 meters inside continuous forest habitats and forest habitat patches (Saunders et al. 1991, 1987). Consequently, effects of mortality lead to fewer trees in disturbed areas and decreased species diversity (Laurance et al. 1997, Laurance et al. 2000).

In addition to decreased diversity and biomass, disturbed forests suffer from several problems associated with botanical reproductive processes. It has been shown that disturbed forests have decreased pollination potential due to lower biomass of potential pollinators (Gigord et al. 1999; Cuningham 2000). Moreover, compounding the potentially limiting

pollination processes, grazing has been shown to significantly decrease the numbers of saplings of key species (Benitez – Malvido 1998, Whitelaw 2001).

Compromised reproductive success in forest plants has a number of instigators. These include both biotic and abiotic forces, a number of which can be lumped into the *edge effects* category. For plants, edges can be a harsh environment. For example, increased levels of UV and wind penetration and unnatural exposure to predators can change the delicate environment plants require in the germination, seedling, and sapling stage and may lead to unfavorable conditions for recruitment (Bruna 2002, Irwin 2006). In addition to these forces, isolation effects and community disruptions also play an important role (Irwin 2006). For example, increased distances between species require extraordinary efforts for pollination and may decrease the probability of successful pollination. Finally, community disruptions occur in both the plant and animal realms. For instance, increasing distances and decreasing natural conditions for pollinators and seed dispersers can lead to a severe negative effect on the availability of pollinators or seed dispersers. Hence, quality and efficacy of service provided by pollinators and seed dispersers can be greatly reduced (Janzen 1983, Cunningham 2000). Furthermore, the abundance of potential predators, such as domestic grazing herbivores and granivores, can also compromise reproductive success in disturbed areas by preying on seedlings and seeds (Benitez-Malvido 1998).

On the other hand, invasive plants can have increased reproductive success in disturbed areas (Janzen 1983). While invasive plants tend to thrive with the compounding effects of edge environments and can frequently withstand the pressure from predators, they also influence the reproductive success of native species. Through competition for resources such as soil nutrients, sunlight, and space, invasive plants often have the competitive edge among seedlings and push

out native seedlings with overcrowding and overshading (Sakai et al. 2001, Daehler 2003, Gordon 1998). This community disruption, in the form of invasive plants, has detrimental effects for the reproductive success of native flora.

In addition to these effects, several studies have suggested that community disruptions may also have significant effects on the timing and prolific nature of reproduction and leaf production in plants (Decker 1994, Irwin 2006, Struhsaker 2008). While effects in the timing and intensity of reproduction can potently influence the reproductive success of individual plants, these types of disruptions have trickle down effects as well. Animal species and communities that depend upon these resources are strongly affected by periods of food scarcity that are the result of disruptions to phenological cycles. Indeed, it has been shown that periods of food scarcity can alter and primarily decrease a habitat's carrying capacity (Brugiere et al. 2002, Irwin 2006). Habitat disturbance can affect phenology and can have within-species changes that affect entire communities (Irwin 2006).

Habitat disturbance can have many abiotic effects on the microclimate of forests (Kapos 1989, Kapos et al. 1997). Physiologists have long studied which abiotic effects are the most potent in affecting a species's phenology, namely photoperiod, the timing of drought, seasonality, temperature and short-term temperature changes (Wright 1996, van Schaik et al. 1993). Within a given species, alterations to the abiotic environment may modify phenology in a protected habitat versus a degraded forest because of the strong effects of abiotic factors, notably UV radiation and water availability (Irwin 2006). Just as it has been noted that tropical plant and tree species synchronize phenophases with various abiotic cues (Rathcke and Lacey 1985), primate species have also been noted to time reproductive and life history events, such as birth, pregnancy, and weaning, with phenophases (Sauther 1998). Disruptions in phenophases,

therefore, can have cascading effects for the entire forest community. Abiotic cues may have a number of effects on plants to trigger phenophases (Irwin 2006). For instance, trees may time young leaf production as more water is available during, or just after, the rainy season when abundant water can facilitate the growth of new tissues. Because seasons are correlated to photoperiod, changes in day length may also trigger plants and trees to coordinate their phenophases with seasons (Singh and Kushwaha 2005, Wright 1996).

The variables connected to the timing of phenophases (production of leaf, flower and fruit parts) are complex (van Schaik et al. 1993). For fruits to mature at the opportune timing in order for a seed disperser to take full advantage, plants must coordinate flowering months prior to this event. The direction of correlation or causality becomes unclear if plants are using abiotic cues to time phenophases to correspond with an increased abundance or activity of pollinators or dispersers. Conversely, plants may have adaptations to avoid higher activity among herbivores or predators (Augsberger 1981). Abiotic cues may also cue reproductive asynchronicity to avoid patterns of predation from herbivores and seed predators. Conversely, plants may use abiotic cues to overwhelm and inundate potential predators via synchronizing all flowering or fruiting phases (Janzen 1971).

Given these complexities of abiotic cues and the timing of delicate phenologic phases, it is not a dramatic leap to assert that disturbance in forest structure may upset the balance of phenology for some species (Kapos et al. 1997). While photoperiod and day length will remain the same in disturbed versus undisturbed forests, changes in other abiotic aspects have been well documented for disturbed forests (Laurance et al. 2002, Laurance and Bierragaard 1997). A host of factors in disturbed forests contribute to changes in soil compaction, shading or lack thereof, and moisture retention. As a result, key abiotic factors such as soil moisture content, irradiation,

and ambient moistures levels are affected. In the event of these factors serving as cues for phenologic phases, disturbed forests may lack the cues to produce key phenologic phases. They may completely disrupt young leaf, flower, or fruit production or cause plants to produce these phases at inopportune times. Indirectly, animal species depending on these resources may in turn adopt different ranging patterns, fall back on Non-traditional food resources, or present behaviors and life history traits that are atypical. Phenology, while understudied in wildlife research (van Schaik et al. 1993), can play a key role in determining the intricacies of animal behavior in disturbed forests.

While the anthropogenic disturbance at Beza Mahafaly tends to dominate much of the discussion in the literature, studies have shown that the compounding effects of natural disasters and anthropogenic disturbance can increase the levels of habitat destruction both spatially and temporally (Ratsimbazafy 2006, Wright 1999). Two important and measurable ways this destruction can occur is in changes to the forest structure and in forest phenology. This critical and emerging issue has received relatively little attention in empirical studies (Bellingham 2008). However, a few authors have noted that natural disturbances (particularly cyclones) could exacerbate the challenges facing organisms in disturbed and fragmented habitats (Dittus 1985a,b; Laurance et al. 2002, Laurance 2002, Laurance and Cochrane 2001, Laurance and Curran 2008, Bellingham 2008, Catterall et al. 2008). Structurally, cyclones can cause devastating damage. Several studies report extensive defoliation, particularly to trees in the upper canopy and emergents (Dittus 1985 a, b, Ratsimbazafy 2006, Bellingham 2008, Catterall et al. 2008). Some research has reported destruction of up to 50% of woody vegetation, mostly in these upper layers (Dittus 1985 a,b; Ratsimbasafy 2006, Catterall et al. 2008). From this research it is clear that high winds have a dramatic destructive effect on trees in the upper canopy with damage in lower

levels primarily linked to tree fellings. Windstorm effects accompanying a cyclone can increase tree-fall gaps, which may lead to an increased number of microenvironments on the forest floor (Catterall et al. 2008). These environments can facilitate forest-floor seedling and herbaceous plant germination. In addition, cyclone disturbance can result in tremendous flooding and landslides, compounding the defoliation and tree loss (Ganzhorn 1995a,b). While it seems logical that fragmented and anthropogenically disturbed discontinuous forests would suffer more damage from cyclones, several studies have shown that anthropogenic disturbance does not exacerbate structural destruction of forests by cyclones. For example, secondary vegetation that developed along two edges of a forest fragment (a road and a power line lane) buffered the interior more effectively than a long-standing natural edge along a stream course in Australia (Bellingham 2008). Furthermore, continuous forest canopies were shown to be just as susceptible to extremely strong cyclonic winds and down-draughts as anthropogenically disturbed forests (Catterall et al. 2008). Finally, cyclones can structurally alter forests – both continuous and disturbed – by facilitating plant invasions (Catterall et al. 2008, Bellingham 2008). These species typically germinate several months after a cyclone's impact, and can be ephemeral.

Phenologically, cyclones can devastate the fruit and flower production in forests long after the cyclone's hit (Dittus 1985a,b; Ganzhorn 1995b, Ratsimbazafy 2006). In turn, cyclone destruction can cause ripple effects and perturbations in ecological processes throughout forest communities. For example, in Sri Lanka, a cyclone dramatically reduced fruit and flower production for two years and caused several resident primate folivores to shift their diet towards new species (Dittus 1985b). Consequently, the overbrowsing of primates on several new species led to increased mortality in several tree species. In Madagascar, cyclone Gretelle had similar

devastating effects on fruit-producing vegetation (Ratsimbazafy 2006). Mean tree crown diameter of fruit trees fed in by lemurs decreased dramatically from 12 meters to 3 meters. This loss translated into a 70% reduction in woody vegetation producing fruit. More recent research at the same site has documented very slow recovery of forest tree species (Ratsimbazafy 2006). While cyclones, and the destructive windstorm forces that accompany the rain and flooding, are undeniably destructive in all types of forests, it remains unclear empirically whether vegetation and forest structure in anthropogenically disturbed forests are more extensively damaged by cyclones than are relatively undisturbed, continuous forests.

The objective of this chapter is to describe the forest structure in each of the habitats I studied, both in and around Beza Mahafaly Special Reserve. I will assess botanical differences between intact, and unprotected areas. In particular, I will discuss the following:

1.) Structural composition of the forests

2.) Species diversity of the forest habitats

3.) Phenological patterns

These quantitative and qualitative descriptions and differences are crucial to interpreting the following chapters that will describe the qualitative differences between ring-tailed lemur groups in these forest habitats.

3.2 Analysis

3.2.1 Data Analysis

To assess differences among protected (Reserve) habitats and disturbed (Non-Reserve) habitats, I used a Kruskal-Wallis one-way analysis of variance to analyze the five transect sites (two in the protected Reserve habitat and three south of the Reserve in the unprotected, disturbed area) (following Siegel and Castellan 1988). The following variables were compared using this

method: distance from sampling point to focal tree as a measure of forest density; tree height; distance of closest shrub to sampling point (another measure of forest density); distance of closest sapling to sampling point; light meter reading; soil compaction; diameter at breast height; number of herbs in plots adjacent to transect points; crown diameter. These data are also presented as median box plots (Figures 3.1 - 3.12) to illustrate the measure of central tendency, importance of outliers, and variation of medians.

To gain a broader understanding of the species distribution, rarity, and commonness in these transects, I applied four measures: overall species richness (S), an index that incorporates the number of species in the transect and their relative abundance (Simpson's Diversity Index, D), the ShanNon-Weiner index of diversity, and species evenness. As species richness and evenness increase, so diversity increases. Moreover, evenness measures the relative abundance of the different species composing the richness of the sampled area. The closer to one, the more even the populations that form the community. In other words, the less variation between the species, the higher the evenness score. Generally, a community dominated by few species (one or two) tends to show less diversity than one in which several different species have a similar abundance. Simpson's Diversity Index is a measure of diversity which takes into account both richness and evenness:

$$D = \sum [n(n-1)]/N(N-1)$$

With Simpson's D, 0 indicates infinite diversity and 1 indicates zero diversity. I will list the results as (1-D) to present the more intuitive form where the greater the value of D, the greater the diversity in that particular area. Simpson's Index gives more weight to the more abundant species in a sample. The addition of rare species to a sample causes only small changes in the value of D. Finally, the ShanNon-Weiner Index is calculated by taking the number of each

species, the proportion each species is of the total number of individuals, and sums the proportion times the natural log of the proportion for each species:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

Because this is a negative number, the equation includes transposing the negative of this sum. When H is high, the habitat exhibits a high level of diversity. Because diversity indices provide more information than simply the number of species present (accounting for some species being rare and others being common), they serve as valuable tools to quantify diversity in a community and describe its structure.

Phenological data are expressed as semimonthly average scores for both protected, Reserve habitats and unprotected disturbed habitats (Figures 3.14-3.17, Table 3.5). As there were three phenology transects, one in the Reserve and two outside of it in disturbed habitats, the average scores for the two transects outside of the Reserve were pooled. These data were analyzed with the Wilcoxon rank sum test, identical to the Mann-Whitney U.

3.3 Forest Physical Structure

3.3.1 Quantitative Physical Structure

Reserve and Non-Reserve habitats have several significant differences in physical structure and forest habitat variables (Table 3.1). The distance from the transect sampling point to focal trees was not different inside the Reserve, but Reserve transects differed significantly from each Non-Reserve, disturbed area transect, except for Non-Reserve 3. This distance measure indicates a significantly larger spread between trees of ≥ 5 cm DBH. There were no significant differences between Non-Reserve 1 and Non-Reserve 2 (indicating a similar distance between trees), and; Non-Reserve 3 and the Reserve habitats. Box plots indicate more variability,

with several noteworthy outliers, outside the Reserve in disturbed areas than in the protected Reserve (Figure 3.1).

Table 3.1 Kruskal-Wallis test results for habitat variables. All values were measured in meters, unless otherwise noted.

Habitat Variable	Mean Rank Reserve 1 (R1)	Mean Rank Reserve 2(R2)	Mean Rank Non-Reserve 1 (NR1)	Mean Rank Non-Reserve 2 (NR 2)	Mean Rank Non-Reserve 3 (NR 3)	Kruskal-Wallis test statistic (corrected for ties)	p-value
Focal tree distance from sampling point	106.438	95.938	142.691	144.583	110.823	19.639	p=0.0006
Focal Tree Height	129.583	163.885	83.989	104.615	117.177	35.571	p<0.0001
Focal Tree Average Crown diameter	119.33	123.375	109.458	138.563	109.26	5.853	p=0.2103
Focal Tree DBH (cm)	123.833	97.698	112.63	140.302	122.75	9.95	p=0.0413
Distance from focal point to sapling	23	14.542	38.227	46.042	26.136	26.082	p<0.0001
Distance from focal point to shrub	9.958	18.583	43.727	43.458	35.417	37.229	p<0.0001
Number of Herbs	85.188	71.938	56.841	41.543	38.583	32.674	p<0.0001
Transect Soil Compaction	42.896	26.479	74.545	90.646	64.188	52.62	p<0.0001
Light Meter Reading	18.045	24.917	44.85	39.792	19.125	23.961	p<0.0001

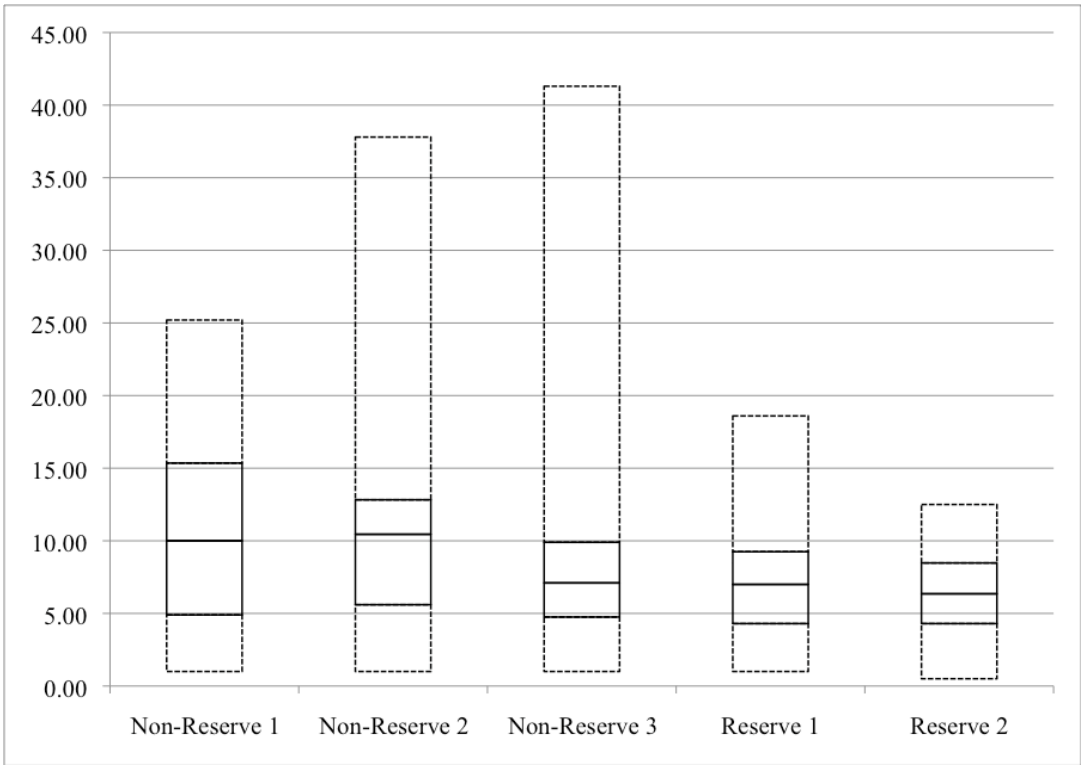

Figure 3.1 Box plot indicating median and ranges of the distance from focal point to focal trees, in meters.

Between habitat transects, tree height measured several significant differences (Figure 3.2). Protected, Reserve habitats showed significantly taller trees when compared to Non-Reserve habitats 1, 2, and 3. Also, between the transects measured inside the Reserve (Reserve habitat 1 and Reserve habitat 2), there appears to be a significant height difference possibly showing the keen differences between gallery habitats and the increasingly dry environment towards the western part of this area. There were also significant differences measured between Non-Reserve habitat 1 and Non-Reserve habitat 2 that are both within the home range of the same group of ring-tailed lemurs, Black Group. The Non-Reserve 1 transect has the shortest trees. Interestingly, Reserve habitat 2 has the greatest variability in tree heights; it is also the transect most embedded in the gallery forest.

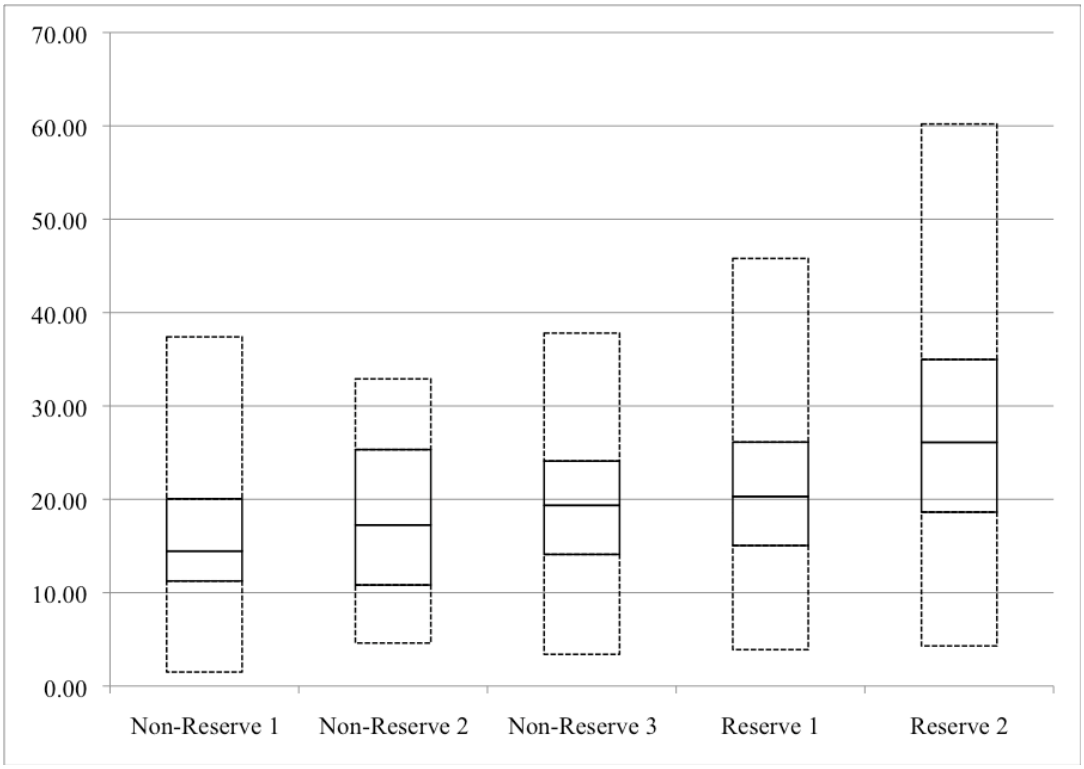

Figure 3.2 Box plot indicating median focal tree heights and ranges in each habitat, measured in meters.

Crown diameter showed no overall significant differences among the habitats. Non-Reserve habitat 2, which is the farthest from the Reserve and is in Light Blue Group's home range, did have larger crown diameters than the other Non-Reserve habitats. Notably, only the Reserve habitats had several trees with such large crowns that they produced data points outside the box plot range (Figure 3.3). Qualitatively, it appears that Reserve Habitats 1 and 2 may have a higher degrees of variability in crown diameter.

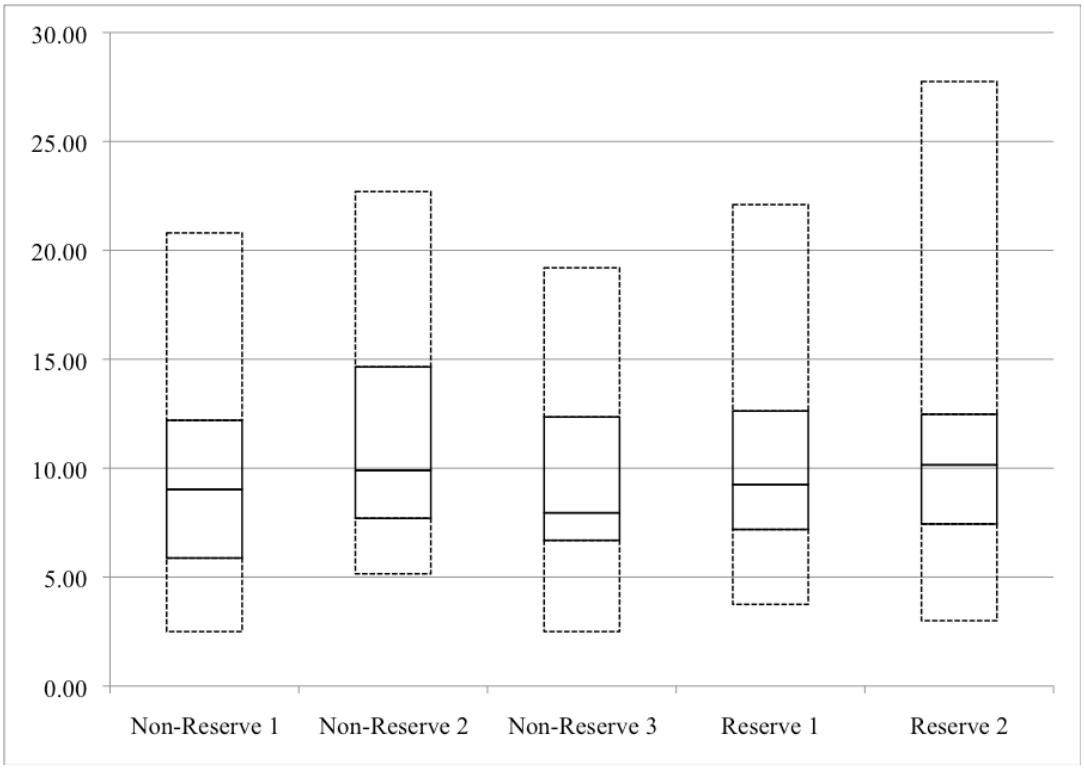

Figure 3.3 Box plot showing median crown diamter and ranges in each habitat in meters.

Among the habitat transects, diameter at breast height illustrated few significant differences. Even among comparisons of gallery versus drier environments, there were few differences. Notably, the smallest diameter trees appear to be in Non-Reserve habitat 3 (primarily Light Blue Group's range); there were significant differences between this habitat and Reserve 2 (Green Group's range) and Non-Reserve 1 (Black Group's range). Habitats within the protected Reserve had several large, outlier data points indicating that this area supports the largest diameter trees in the area sampled (Figure 3.4). It is important to note that there are a larger number of old growth trees in the habitats along the Sakamena – regardless of the Reserve boundaries. These trees are more difficult to cut down, and are sometimes culturally protected (Whitelaw, unpublished data).

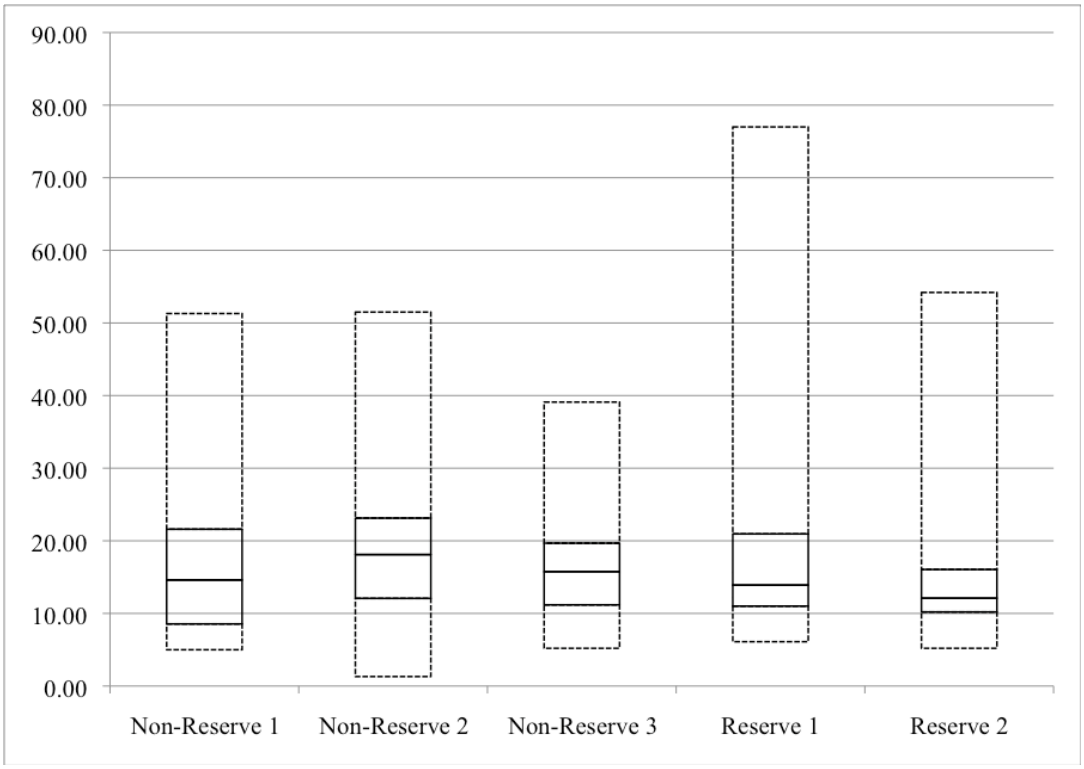

Figure 3.4 Box plot showing median diameter at breast height (in cm) and ranges for focal trees in each habitat.

Measurements of the distance of the sampling point to the nearest shrub showed a high degree of significance when comparing Reserve habitats to habitats outside the protected region. Indeed, both Reserve habitats were highly significant ($p<0.0001$) when compared to each Non-Reserve habitat. Non-Reserve habitat 2 showed the greatest range of variability of sampling point distance to nearest shrub (Figure 3.5). Reserve one and two were the most consistent in distances to shrubs (Figure 3.5).

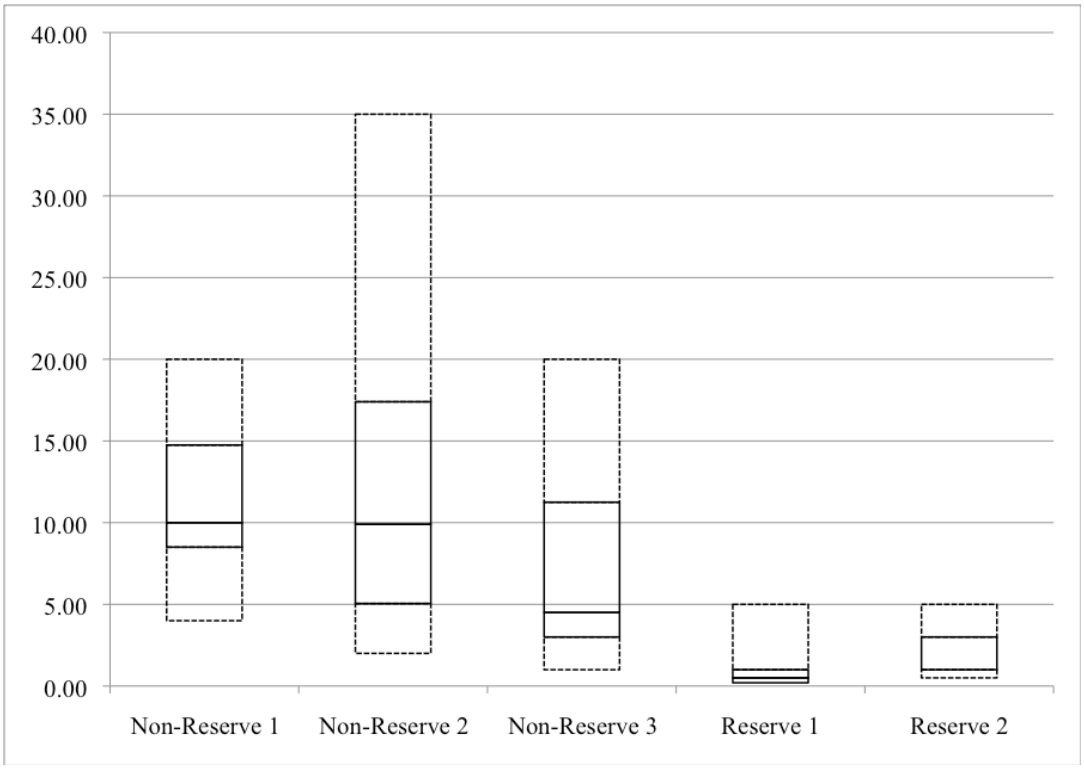

Figure 3.5 Box plot indicating median and ranges of distances from focal point to shrubs in each habitat in meters.

Measurements of the distance from the sampling point to the nearest sapling had similar results to the nearest shrub measurements. Reserve habitats were significantly different from each Non-Reserve habitat with the exception of Reserve 1 and Non-Reserve 3, again indicating that this habitat appears to have some protected habitat qualities. These measures indicate that protected habitats have a denser and more frequent occurrence of saplings. Of the unprotected habitats, Non-Reserve 3 has the least distance from sampling point to sapling, and Non-Reserve 1 and 2 show no significant difference in their distance from sampling point to sapling (Figure 3.6).

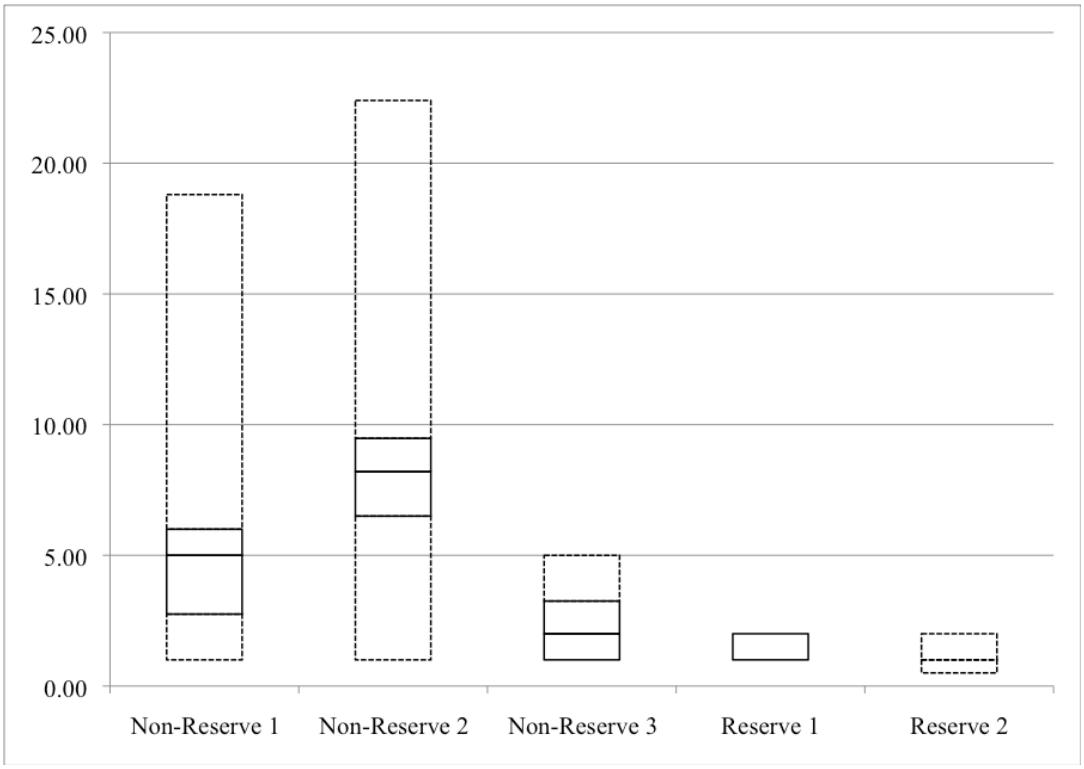

Figure 3.6 Box plot indicating median and ranges of distances from focal point saplings.

Similarly, the Reserve habitats had significantly higher number of herbs than most of the Non-Reserve habitats. Specifically, Reserve 1 transect had more herbs than all of the Non-protected habitats ($p<0.0001$). Reserve 2 transect had more herbs than Non-Reserve 2 and 3 transects. These transects are the farthest from the protected, fenced Reserve. The only significant difference between Non-Reserve habitats was between Non-Reserve 1 and Non-Reserve 3; two transects that lie next to each other. Qualitatively, the Reserve habitats had the highest variability in the number of herbs sampled (Figure 3.7).

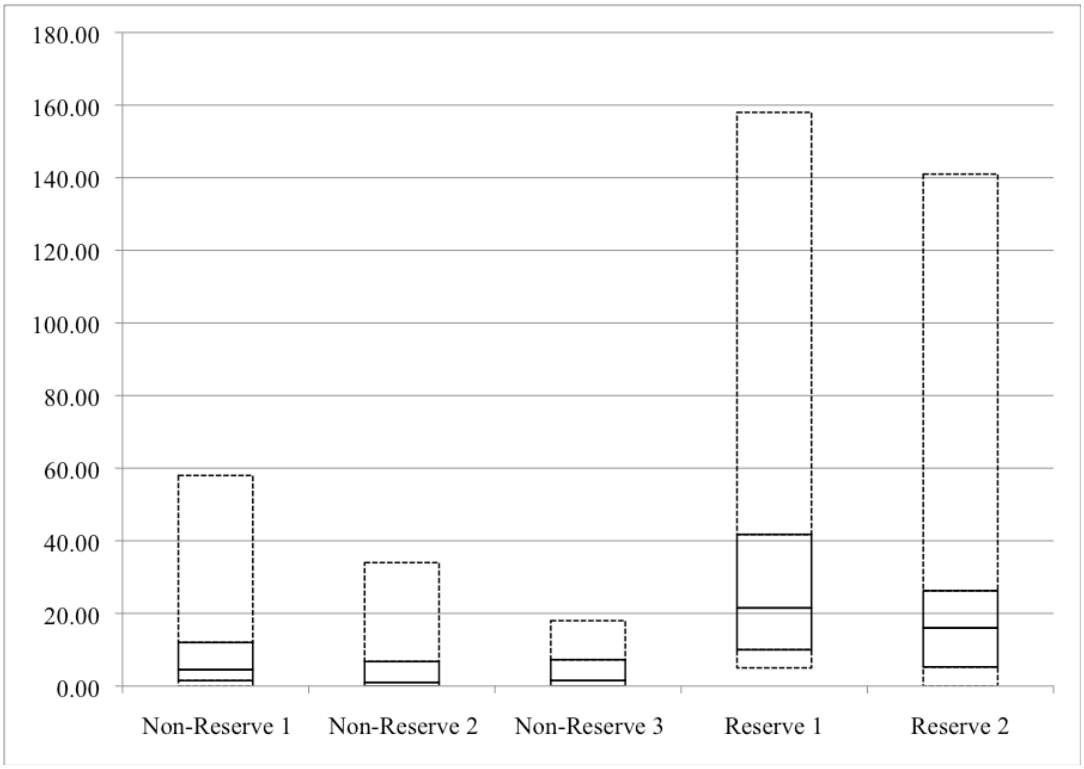

Figure 3.7 Box plot indicating number of herbs present in each habitat's sample.

Soil compaction was significantly higher in the habitats with the most human traffic ($p<0.0001$). Specifically, Non-Reserve 1 overlaps with the research camp and several foot trails, and Non-Reserve 2 includes foot trails, greater grazing incidences, and an ox-cart road. Reserve habitats indicated little to no soil compaction, with Non-Reserve 2 having the highest degree of compacted soil (Figure 3.8). Non-Reserve 1 and Non-Reserve 3, which are closest to each other outside of the Reserve were the most similar in soil compaction measurements. Once again, Reserve 1,2, and Non-Reserve 3 were the most similar in compaction measurements and also contained several outlier points (Figure 3.8).

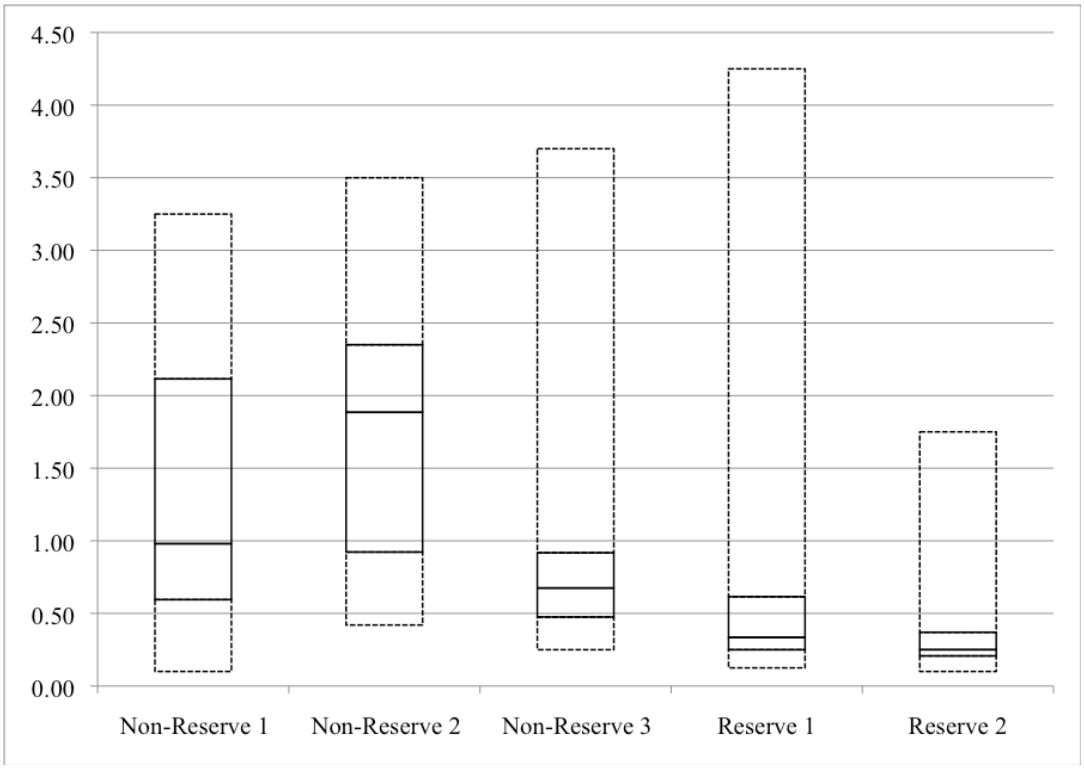

Figure 3.8 Box plot indicating median and ranges of soil compaction measurements.

Finally, light meter measurements illustrated that whereas Reserve habitats were quite similar to each other, likewise were Non-Reserve habitats 1 and 2. Non-Reserve habitats 1 and 2 had significantly higher light meter readings than both of the Reserve habitats and Non-Reserve 3. Again, Non-Reserve 3 showed similarities to the protected Reserve (Figure 3.9).

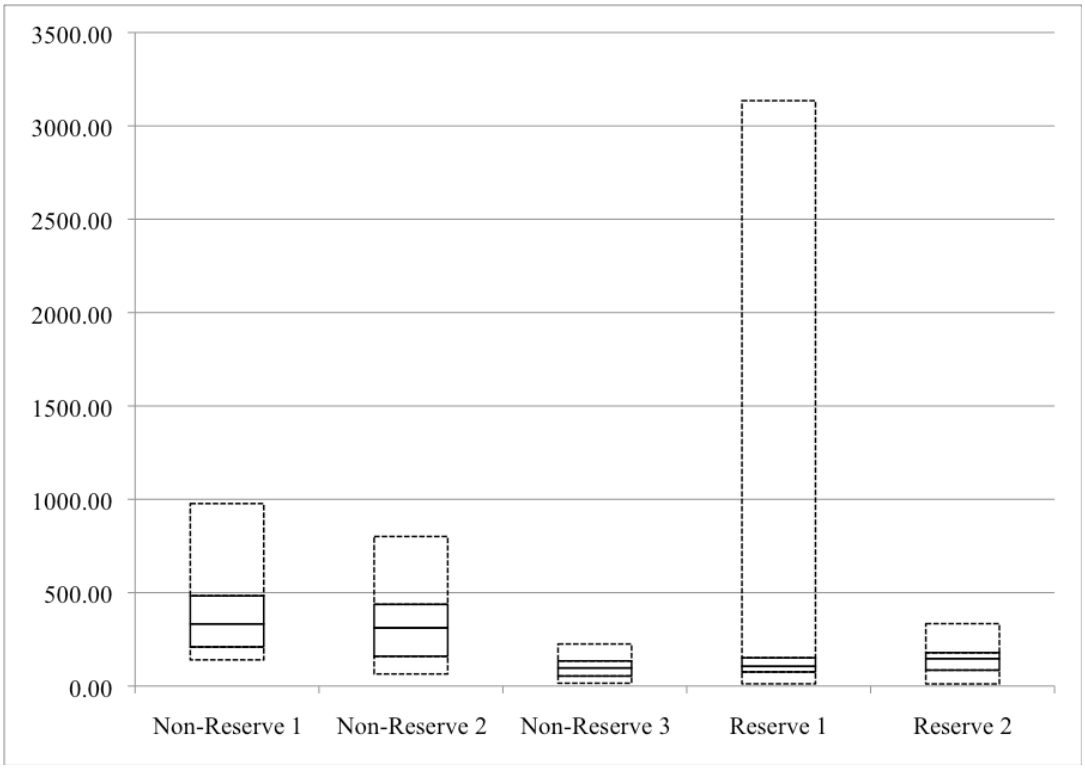

Figure 3.9 Box plot indicating median and ranges of light meter readings in each habitat.

Reserve 1 and 2 have significantly higher numbers of both *Tamarindus indica* and *Azima tetracantha* saplings than each of the Non-Reserve habitats (Table 3.2; Figures 3.10, 3.11). These are perhaps the most alarming and disparate measures of habitat measurements as they are indicative of the future composition of key ring-tailed lemur food species. Additionally, there are significantly more vines available inside the Reserve – a result that will be revisited in the feeding ecology chapter (Figure 3.12, Table 3.2). Finally, Non-Reserve habitats have a significantly higher incidence of zebu feces, which is a strong indicator of grazing presence (Table 3.2, Figure 3.13).

Table 3.2 Kruskal-Wallis results for comparisons of *Tamarindus indica* sapling, *Azima tetracantha* sapling, vines, and zebu feces presence in all habitats.

Variable	**Kruskal-Wallis test statistic**	**P-value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
# of *Tamarindus indica* saplings present	30.840	0.0001	Y	Y
# of *Azima tetracantha* Saplings	29.773	0.0001	Y	Y
Zebu feces present	33.574	0.0001	Y	Y
Number of vines present	39.082	0.0001	Y	Y
# of *Quisivianthe papionae* sapling present	18.300	0.0001	Y	Y

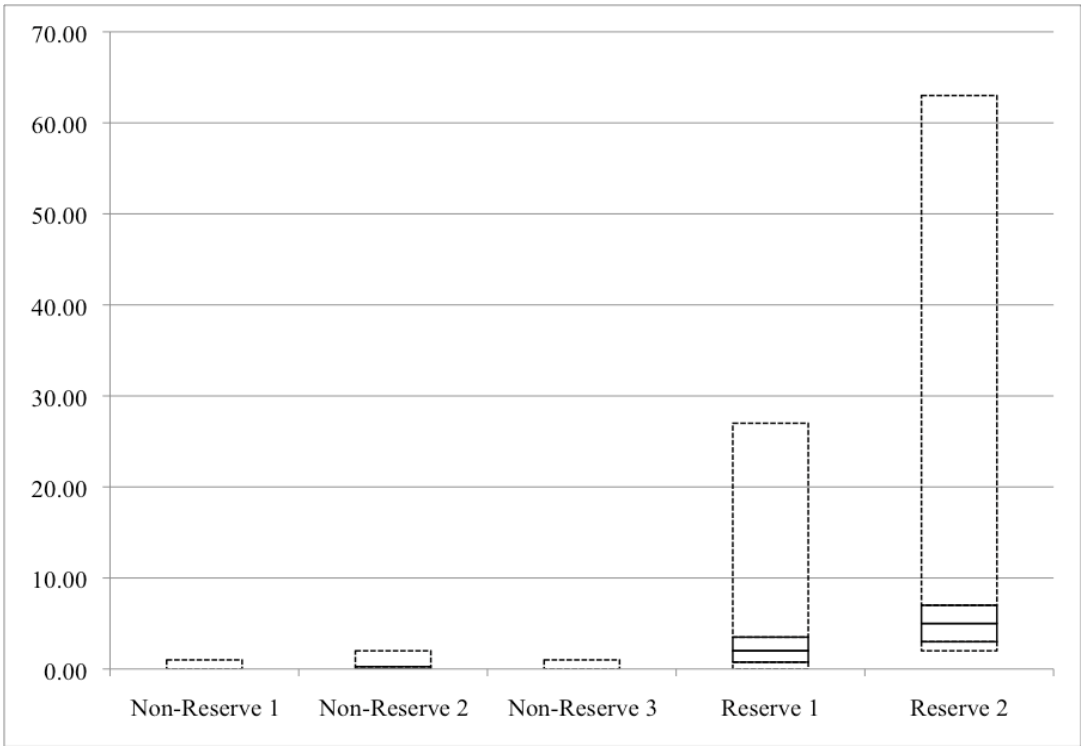

Figure 3.10 Box plot indicating median number and ranges of *Tamarindus indica* saplings in each habitat.

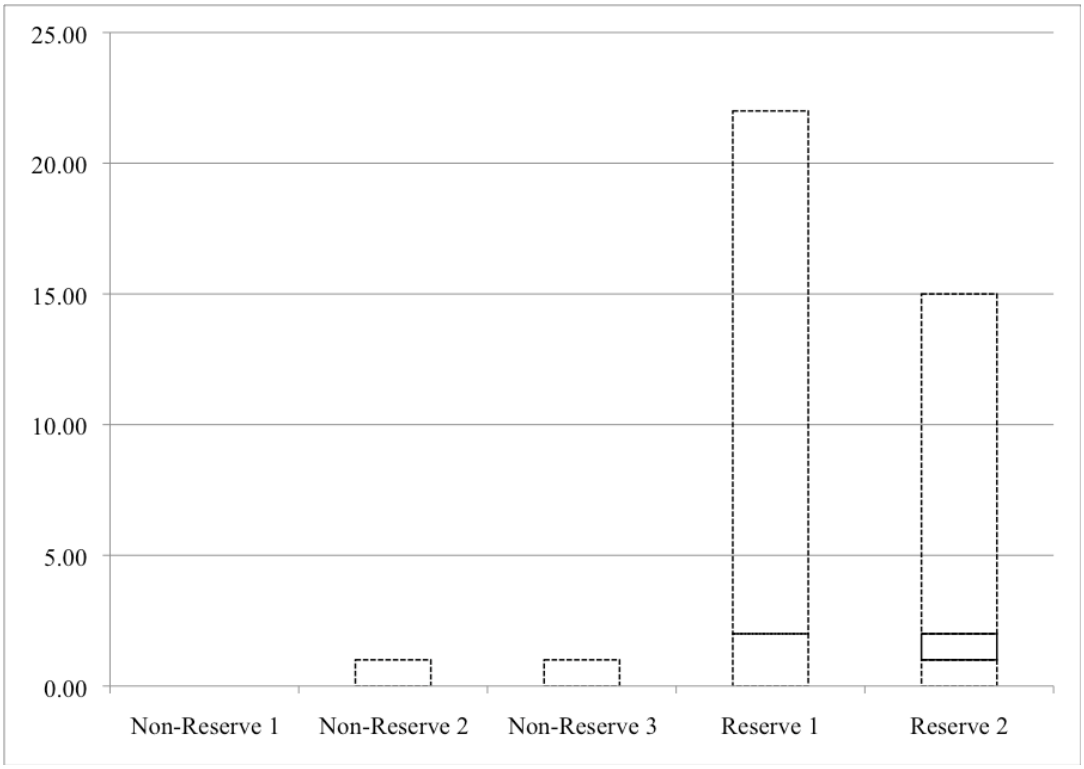

Figure 3.11 Box plot indicating median number and range of *Azima tetracantha* saplings present in each habitat.

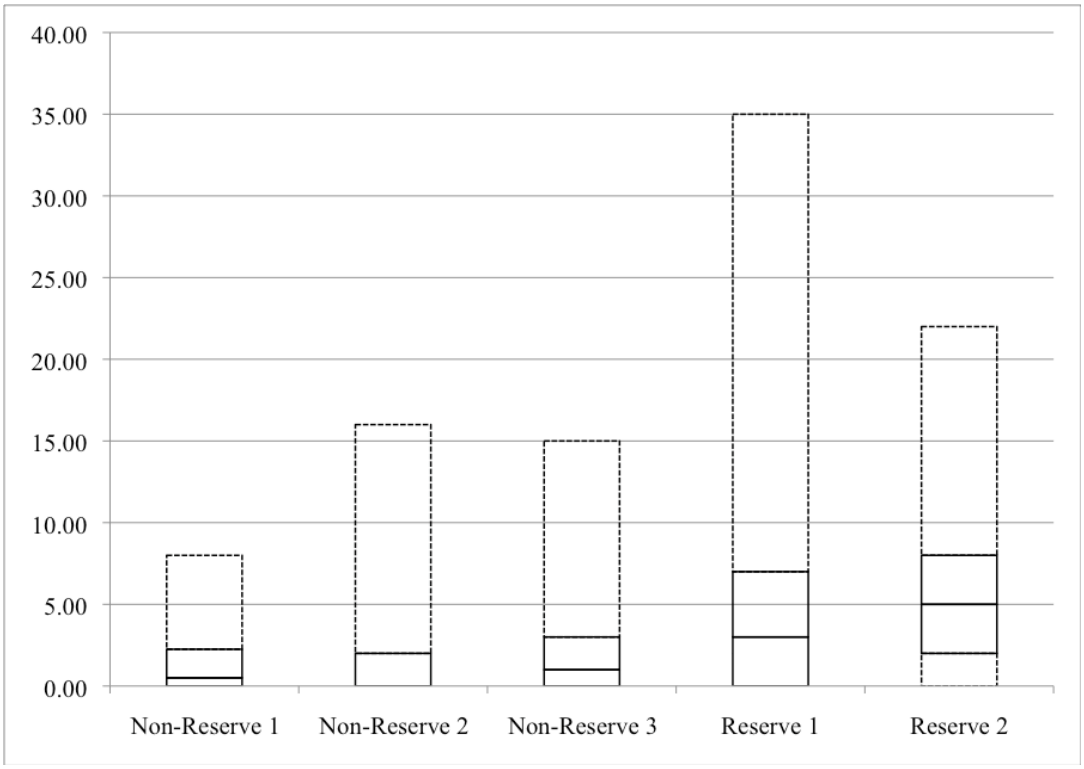

Figure 3.12 Box plot indicating median number and range of vines present in each habitat.

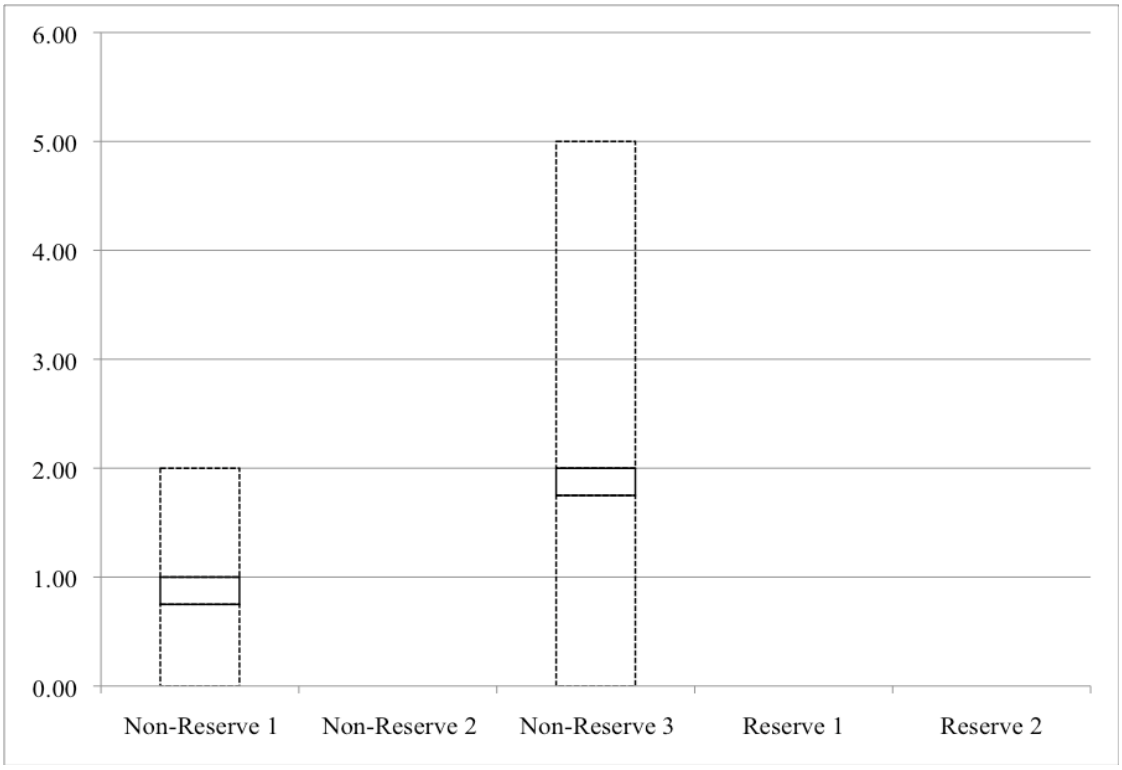

Figure 3.13 Box plot indicating median number and range of zebu feces present in each habitat.

Finally, Non-Reserve habitats show an overall significantly higher number of anthropogenic variables (Table 3.3). These include higher levels of evidence of tree harvesting; presence of paths, trails, and roads; higher likelihood of agricultural activity near the habitat; and a greater likelihood that the canopy will not be connected at the focal point of the habitat transect. These results show an overall increase in anthropogenic activity in Non-Reserve habitats that can have a compounding effect on lemur ecology as will be examined in the next chapters.

Table 3.3 Results of Wilcoxon rank sum test examining presence of agriculture, paths/roads, tree harvesting, and canopy connectedness.

Anthropogenic or Habitat Variable	Value of Wilcoxon rank sumTest Statistic	P-Value	Reject H_0 at 1% significance level?	Reject H_0 at 5% significance level?
Presence or absence of agricultural crops	2.279	0.0227	N	Y
Number of paths/ trails/roads present	6.065	0.0000	Y	Y
Presence or absence of tree harvesting	7.681	0.0000	Y	Y
Presence or absence of connected canopy at focal point	-10.785	0.0000	Y	Y

3.4 Species Diversity and Composition

There were no marked differences between diversity indices in each of the sampled habitats (Table 3.4). According to the diversity indices, Non-Reserve habitats tended to be slightly more diverse than the Reserve habitats. The Simpson's diversity index indicated the following order, ranked from most to least diverse: Non-Reserve 2, Non-Reserve 1, Reserve 2, Non-Reserve 3, and Reserve 1. The ShanNon-Wiener index varied only slightly from this pattern: Non-Reserve 1, Non-Reserve 3, Reserve 2, Non-Reserve 2, and Reserve 1. Analogous to the previous forest structure results, Non-Reserve 3 is more similar to the Reserve habitats, more so than the other unprotected habitats. This result shows that Non-Reserve 3 is perhaps buffered by its close proximity to the Reserve. In terms of species richness, habitats outside the Reserve are higher in the number of tree species present. This result might result from high turnover of plants due to species being cut down, thus altering the more natural succession in these forests. Species richness reaches its highest score in Non-Reserve 1 (Black Group's habitat) and Non-Reserve 3 (primarily Black Group's home range). In terms of forest species

evenness, Reserve 2, Non-Reserve 1 and Non-Reserve 2 had the least variation in species. Reserve 1 showed the most variation in evenness. Evenness represents the relative abundance with which each species is represented in an area. A forest where all the species are represented by the same number of individuals has high species evenness. A forest where some species are represented by many individuals, and other species are represented by very few individuals has a low species evenness. In these results, it appears that Reserve habitats tend to be more even.

Table 3.4 Diversity index results for all transects.

Index	Reserve 1	Reserve 2	Non-Reserve 3	Non-Reserve 2	Non-Reserve 1
ShanNon-Wiener Index	1.0522683	1.3729048	1.3977079	1.3534623	1.5538353
Richness	6	7	9	6	9
Simpson D	0.4409722	0.35069445	0.3967014	0.3125	0.3298611
Simpson 1-D	0.5590278	0.6493056	0.6032986	0.6875	0.6701389
Evenness	0.58728206	0.7055335	0.63612425	0.7553817	0.7071809

3.5 Phenology of Reserve and Non-Reserve Habitats

3.5.1 Seasonal patterns of plant part availability

Both habitats, inside and outside of the protected BMSR area, showed distinct seasonal patterns of the availability of plant parts (Figures 3.14-3.17). Leaf buds and young leaves were most available from October – November, with another spike at the end of the rainy season, February – April. Flower buds and flowers followed a similar pattern. Fruits were most available towards the end of the wet season and hitting a peak in March. For all phenophases, there is a distinct season of low availability in June – October, which corresponds directly to the coolest and driest portion of the year. As mentioned previously, the BMSR region suffered a significant cyclone during January, 2005, nine months before the start of this study. This cyclone

presented with high winds and record levels of flooding. Phenological data collected in Parcel 1 by the Beza Mahafaly ecological monitoring team and research director of BMSR describe a severe decrease in the number of flowering kily trees (*Tamarindus indica*) due to this significant storm. Based on their data, there were no tamarind fruit available within parcel 1 during the dry season of 2005 (Jacky Youssouf, pers. comm). Apparently, the timing of the storm occurred during the flowering phase of many kily trees. This may have played a part in the phenology of the early part of this study (October – November), which is also the driest and most resource-depleted time of year for the ring-tailed lemur. Undoubtedly, the cyclone affected the phenology of this area, compounding anthropogenic disturbance.

3.5.2 Differences among habitats in resource availability

The overall pattern of seasonality and reproductive timing between Reserve and Non-Reserve habitats is similar (Figures 3.14, 3.15). There are, however, differences between these habitats in the levels at which these resources are produced. Table 3.6, shows Wilcoxon rank sum results for phenological comparisons between Reserve and Non-Reserve habitats and indicates that there is a significant difference in fruit availability between the habitats, with Non-Reserve transects showing more fruit availability ($p < 0.0144$). While resource availability was overall consistently less in the Reserve habitats, it was only significantly less for fruits and flowers. These results indicate that during the study period, trees sampled in the disturbed, unprotected habitat have more availability of these resources. While Non-protected habitats appear to have higher scores throughout the study period, it is important to note that resources appear to be more evenly and consistently available for lemur groups residing within protected habitat. Also important is that phenology transects outside the Reserve were located in edge habitat. Many of these trees sampled were mature, large DBH, large crown diameter kily trees

due to the lack of other trees in the area (smaller DBH trees tend to be the first to be cut). Further, most of the Non-Reserve phenological data were collected from kily trees and could reflect effects from the cyclone earlier in the year (Table 3.7). The higher incidence of kily trees sampled may have influenced these results, because they were usually the only tree available (19 sampled in the Non-Reserve transect, vs. 12 in the Reserve transect). Indeed, within the Reserve only 29% of fruit trees sampled were kily but in the Non-Reserve 73% of fruit trees sampled were kily. Also, because these trees tended to be located in the edge habitat in the Non-Reserve habitats, their productivity may be increased due to the increased exposure to sun, lack of competition with other trees in the disturbed area, and resource availability. Furthermore, the kily trees in the disturbed areas were buffered from the effects of the cyclone because of their distance from the river. Kily trees in the Reserve suffered the highest direct wind damage and flooding. Perhaps as a consequence, only half of the trees sampled in the Reserve produced fruit during the study period (Figure 3.16). Finally, it is important to note again that all of the trees sampled were of similar DBH, large, and mature trees, therefore there are probably minimal anthropogenic effects for these larger trees, but possible edge effects.

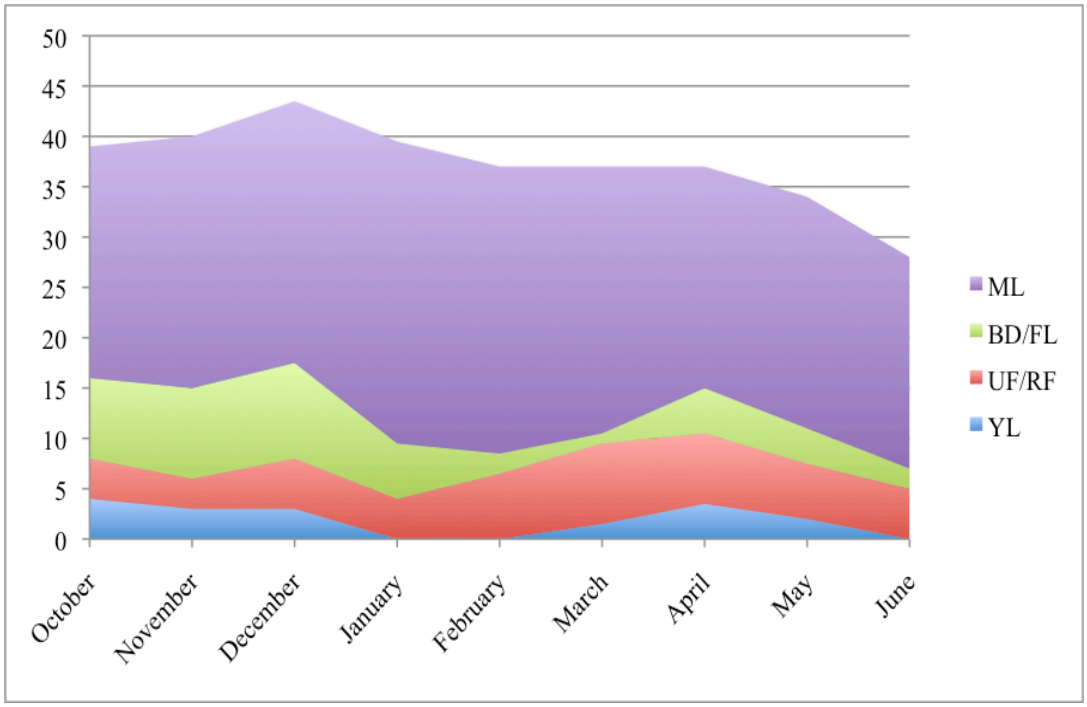

Figure 3.14 Monthly results of phenology scores for Reserve habitats. YL = young leaves, UF/RF = fruit scores, BD/FL = flower buds, ML = mature leaves. Y-axis indicates the total score for each phenological phase. Higher scores indicate more abundance for that particular resource.

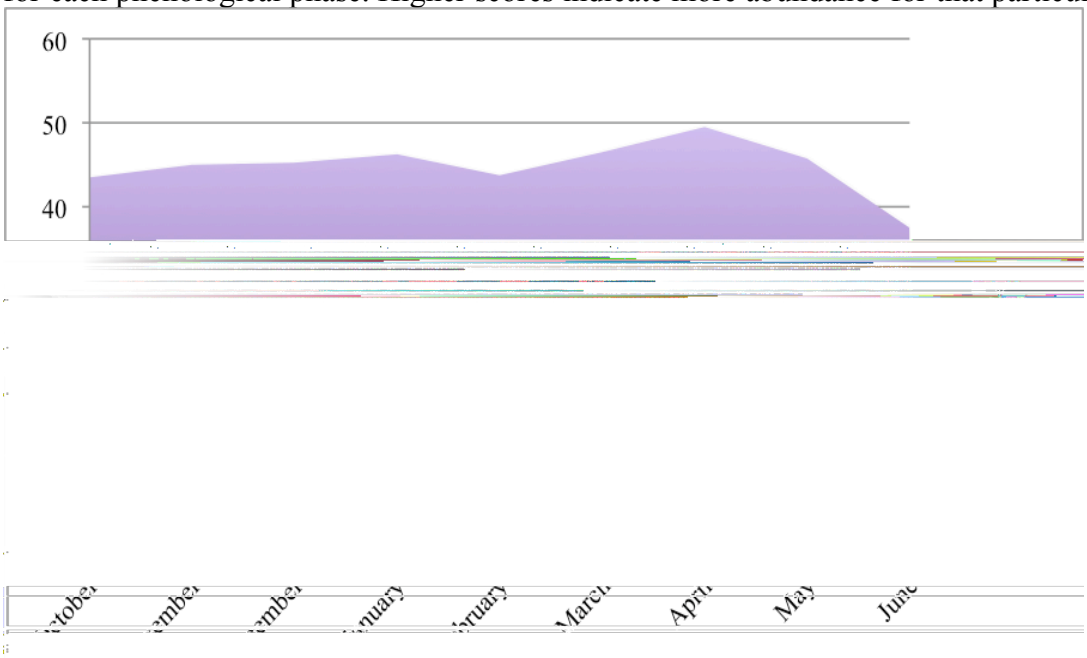

Figure 3.15 Monthly results of phenology scores for Non-Reserve habitats. YL = young leaves, UF/RF = fruit scores, BD/FL = flower buds, ML = mature leaves. Y-axis indicates the total score for each phenological phase. Higher scores indicate more abundance for that particular resource.

Table 3.6 Wilcoxon rank sum results for monthly phenological score comparisons

	Young Leaves total scores		Mature Leaves total scores		Dry Leaves total scores		Flower Buds total scores	
Month	Reserve	Non-Reserve	Reserve	Non-Reserve	Reserve	Non-Reserve	Reserve	Non-Reserve
October	4	2	23	27	1	1	7	12.5
November	3	1.5	25	27.5	1	1	8	5
December	4	1.5	24	27	1	0.5	5	4.5
December	2	0.5	28	29	0	0.5	1	0.5
January	0	0.5	30	27.5	0	0	2	3.5
January	0	0	30	30	0	0	2	2
February	0	0	30	30	0	0	0	0.5
February	0	4	27	26	3	0	1	0
March	0	6	29	24	1	0	1	0
March	3	7	24	23	3	0	1	4.5
April	2	7.5	23	22	5	0.5	4	4.5
April	5	7.5	21	22	3	0.5	2	0.5
May	4	2.5	21	26.5	3	1	1	0.5
May	0	0	25	28.5	2	1	1	0
June	0	0	21	25.5	5	4	2	0
Wilcoxon rank sum test statistic		20.5		27.5		1.5		42.5
p-value		0.1851		0.3268		0.008		0.2348

Table 3.6 continued

	Mature Flowers total scores		Dry Flowers total scores		Unripe Fruit total scores		Ripe Fruit total scores	
Month	Reserve	Non-Reserve	Reserve	Non-Reserve	Reserve	Non-Reserve	Reserve	Non-Reserve
October	1	0.5	0	0	0	0.5	4	1
November	1	7.5	0	0.5	0	0	3	2.5
December	5	8.5	0	0.5	0	0.5	4	2
December	8	12.5	0	0	3	4	3	0
January	3	3	0	1	2	9.5	1	1.5
January	4	2.5	0	0.5	4	10	1	2.5
February	1	2.5	2	1	0	0.5	6	11.5
February	2	0.5	0	1.5	0	1	7	11
March	0	0.5	1	0	1	0	7	13
March	0	0.5	0	0	0	0.5	8	14
April	0	3.5	0	0	0	0	8	11
April	3	8	0	0	0	0.5	6	11
May	3	7.5	0	0.5	1	0	5	9.5
May	2	7	0	1	0	0	5	9.5

June	0	6.5	0	0	0	0	5	5.5
Wilcoxon rank sum test statistic		12		13		15		21
p-value		0.0088		0.2604		0.1394		0.0072

Table 3.7 Species List for Reserve and Non-Reserve Phenology Transects

Number of Individuals	Species Name	Type of specimen
	RESERVE TRANSECT	
4	Tratraborondreo – *Grewia leucophylla*	Tree
10	Filo filo – *Azima tetracantha*	Bush
2	Hazombalala – *Rinorea angustifolia*	Tree
2	Taly – *Terminalia seyrigii*	Tree
2	Daro – *Commiphora aprevalii*	Tree
12	Kily – *Tamarindus indica*	Tree
2	Daromangily – *Commiphora grandifolia*	Tree
4	Mantsaka – *Tarenna pruinosum*	Bush
8	Valiandro – *Quivisianthe papinae*	Tree
2	Akaly – *Crateva excelsa*	Tree
2	Sasavy – *Salvadora angustifolia*	Tree
4	Dango – *Talinella grevei*	Bush
6	Tratriotse – *Talinella grevei*	Tree
		Bush – 3 total Tree – 10 total
	NON-RESERVE TRANSECT	
19	Kily – *Tamarindus indica*	Tree
10	Filo filo – *Azima tetracantha*	Bush
1	Daro – *Commiphora aprevalii*	Tree
5	Kotipoke – *Grewia grevei*	Tree
2	Dango – *Talinella grevei*	Bush
6	Sasavy – *Salvadora angustifolia*	Tree

4	Mantsake – *Enterospermum pruinosum*	Bush
1	Tsikidrakatse - *Bridelia sp.*	Tree
7	Valiandro – *Quivisianthe papinae*	Tree
4	Tratriotse – *Acacia bellula*	Tree
1	Katrafay – *Cedrelopsis grevei*	Tree
		Bush – 3 total Tree – 9 total

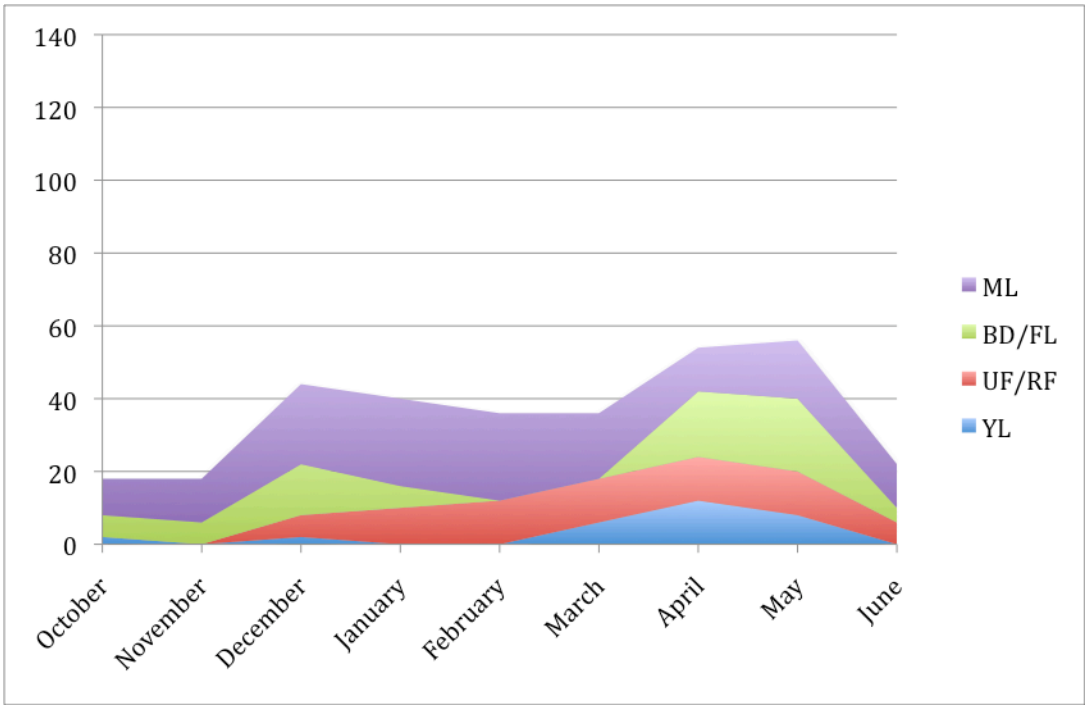

Figure 3.16 Monthly results of phenology scores for Reserve habitat *Tamarindus indica* trees. YL = young leaves, UF/RF = fruit scores, BD/FL = flower buds, ML = mature leaves. Y-axis indicates the total score for each phenological phase. Higher scores indicate more trees with that particular phase.

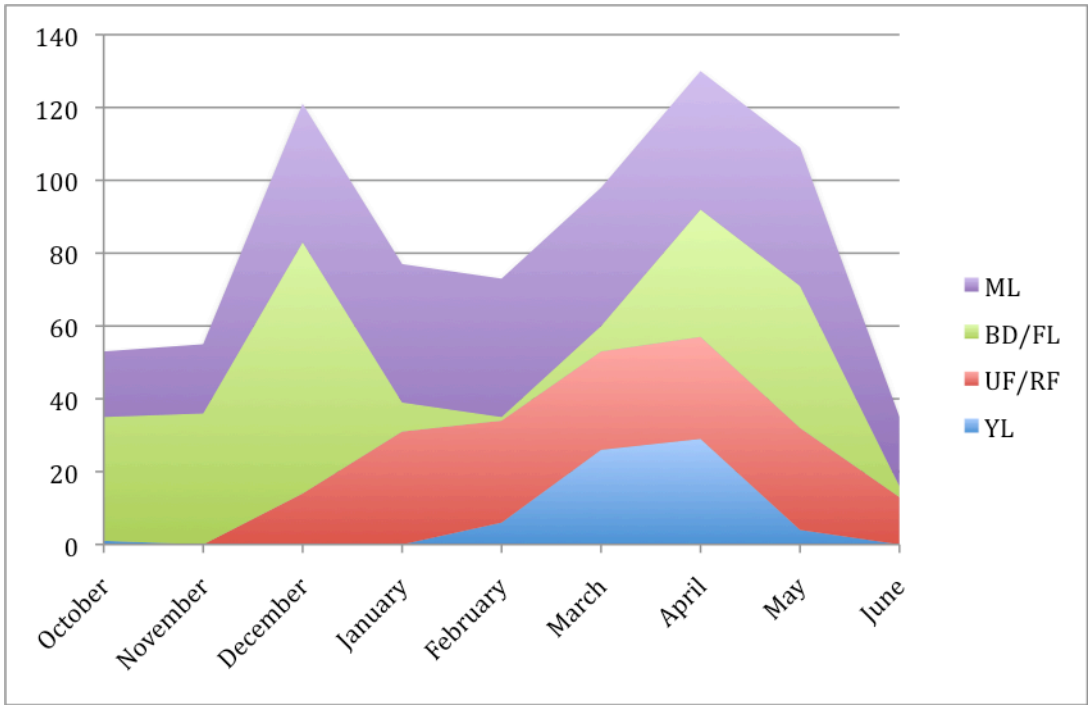

Figure 3.17 Monthly results of phenology scores for Non-Reserve habitats. YL= young leaves, UF/RF = fruit scores, BD/FL = flower buds, ML = mature leaves. Y-axis indicates the total score for each phenological phase. Higher scores indicate more trees with that particular phase.

3.6 *Tamarindus indica* Phenology and Key Comparisons to 1987-88.

Tamarind trees, locally known as "kily", have been well-documented as a key resource for *L. catta* in gallery and dry forest habitats (Sauther 1992, Gould 2006). In fact, because a preference for *T. indica* has been shown in a variety of habitat and sites, it has been described as a 'dominant' food and all other foods are secondary in these habitats (Yamashita 2002, Gould 2006). In terms of forest structure in and around BMSR, *T. indica* trees dominate the gallery forest in both the Reserve and other areas. Recently, *T. indica* has been described as a fallback food for *L. catta* (Sauther and Cuozzo 2009), meaning that its use is negatively correlated with the abundance of preferred foods. Lemur feeding ecology and phenology has been documented as highly consistent for Non-drought years (Sauther and Cuozzo 2009, Yamashita 2008, Ratsirarson et al. 2001). This dissertation has the advantage of having comprehensive

comparative phenological data from 1987-88 (Sauther 1992). This data set was recorded during a Non-drought and Non-catastrophic cyclone year – a relatively stable year. I will use these data for several key comparisons of both phenology and feeding ecology. These comparisons are general qualitative discussions because methodology differed enough to make direct quantitative comparisons unreliable.

While phenology and feeding ecology of *L. catta* and its habitat tend to be fairly predictable, there are a number of notable differences during the post-cyclone cycle. During 1987-88 (a Non-drought and Non-destructive cyclone year), *T. indica,* young leaves were available for all months except July and August. During 2005-06, there were no young leaves available until March, when abundance levels during March and April were similar to 1987-88 (Table 3.7). This protein resource was thus not available during the early and mid lactation period of 2006. Flower production followed a similar schedule between the two comparison years – it appears that flower production had returned to typical levels when my study period began, about nine months after the cyclone. Significantly, the 1987-88 dataset illustrates two different patterns with regards to *T. indica* fruiting patterns. First in 1987-88 *T. indica* fruit was available throughout the entire year, with fluctuations in levels. During 2005-06 there were a full four months with no *T. indica* fruit being available. Second, during my study it appears that the availability of tamarind fruit was shifted to the late wet season-early dry season (March - June) when compared to 1987-88 (Table 3.8; Figures 3.18, 3.19, 3.20). Upon my arrival at BMSR in September of 2005, there were no *T. indica* trees fruiting. Four months passed and the rainy season had begun before this fruit emerged during the late wet season of 2006. This key difference is probably linked to the loss of flower production during the early part of 2006,

which led to a failure of *T. indica* fruit during the dry season of 2006. As the wet season began, flower production proceeded again under more typical, non-catastrophic, conditions.

Table 3.8 *T. indica* phenology comparisons between 2005-06 and 1987-88. Phenological scores run from 4 (abundant) to 0 (absent).

	2005-06	2005-06	2005-06	1987-88	1987-88	1987-88
Month	Young Leaves	Flowers	Fruit	Young Leaves	Flowers	Fruit
October	0	2	0	2	0	2
November	0	3	0	2	3	2
December	0	3	0	1	3	2
January	0	0	1	1	2	2
February	0	0	2	1	0	3
March	2	0	3	1	0	1
April	2	2	3	4	0	1
May	2	1	3	1	1	1
June	0	1	3	1	1	1
July	-	-	-	0	1	2
August	-	-	-	0	1	3
September	0	0	0	1	1	3

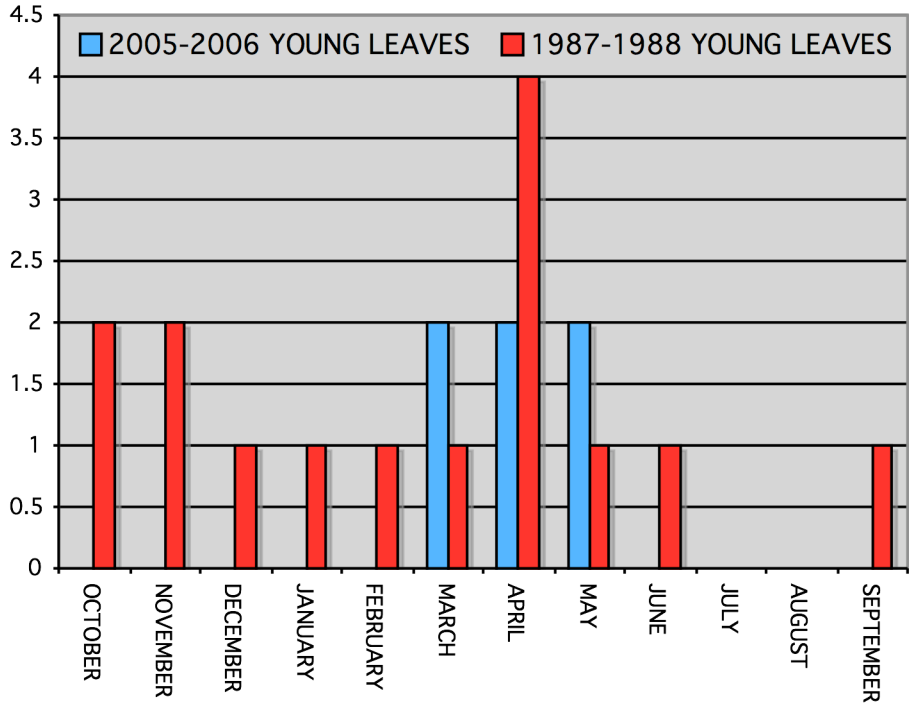

Figure 3.18 Comparison between 05-06 and 87-88 study years of *T. indica* phenology: young leaves.

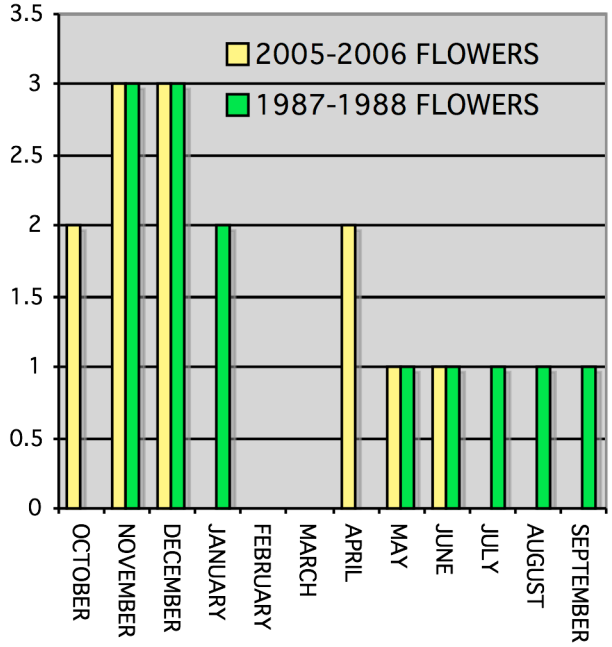

Figure 3.19 Comparison between 05-06 and 87-88 study years of *T. indica* phenology: flowers.

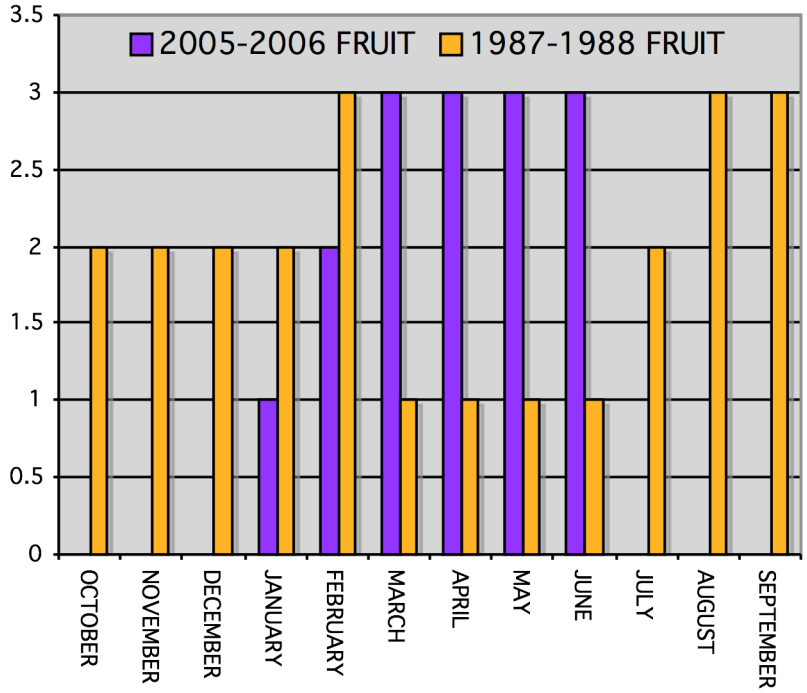

Figure 3.20 Comparison between 05-06 and 87-88 study years of *T. indica* phenology: fruit

Two other key resources documented in 1987-88 were very different phenologically in 2005-06. First, *Salvadora angustifolia*, a key fruit eaten during October and November in 1987 (the very end of the dry season, and early beginning of the wet) produced hardly any fruit during my study period. These trees are abundant in all *L. catta* areas that were monitored twice each month for phenophase changes. Second, *Enterospermum pruinosum*, a key fruit consumed the dry months of May-July in 1988, was available and consumed much later, during November and December of 2005. Again, it appears that for important resources – *T. indica, S. angustifolia,* and *E. pruinosum*, the catastrophic cyclone of 2005 disrupted both the timing of phenophases and production all around for vital *L. catta* food species.

3.7 Impact of Anthropogenic Disturbance

Qualitative assessments of each of the habitats revealed higher average levels of disturbance in Non-protected areas. For instance, in Non-Reserve habitats, focal trees (trees

closest to the sampling point) were more often cut or stripped – an indication of harmful human activity in these areas. Furthermore, transects in the Reserve more often passed through large patches of herbs and groves of *Grewia* species – both important food resources for *L. catta*. Non-Reserve transects rarely, if ever, passed through herb patches, dense undergrowth, vines, and saplings. If there were patches of these, then there were also signs of grazing that limited their presence. In addition, transects outside of the Reserve were more likely to pass through livestock trails, human footpaths, or roads. A further indication of disturbance in Non-Reserve habitats was the presence of stumps in close vicinity to the sampling points. The presence of an understory, also quantified above with the measurements of nearest sapling and nearest understory bush, was usually absent in the Non-Reserve habitats. These transect areas were frequented by local people in their local travel, with grazing herds, and general use. Clearly, habitats inside the Reserve possess multiple layers of resources for *L. catta*: terrestrial herb patches, understory of bushes (primarily *Azima tetracantha* bushes), and the higher canopy. In one Non-Reserve habitat transect, qualitative notes indicate that there were five stumps measuring a DBH of eight within five meters of the sampling point. In addition, at this sampling point saplings were at least 10 meters apart, bushes were at least 15 meters apart quantifying the incredibly sparse understory and homogeneous canopy layer. Habitats outside of this protected area 1.) lack the complexity of layers, 2.) have a higher degree of anthropogenic presence and disturbance, and 3.) lack the sapling recruitment to sustain forest heterogeneity and complexity in the future.

3.8 Discussion

The data presented in this chapter provide a foundation for interpreting chapters to follow. These results show that Reserve and Non-Reserve habitats differ in multiple and

complex ways. Results are also quite similar to the pilot study conducted in 2001 that compared habitats inside and outside BMSR with many of the same methods. Both of these studies found significant differences between protected and anthropogenically disturbed habitats. For example, in terms of forest density, larger DBH trees, saplings, and shrubs, which are each important components of forest stratification, are significantly denser in Reserve habitats. These attributes provide several layers of information: these forests have multiple canopies providing significantly more resources in terms of diet, arboreal pathways, sleeping sites, predator evasion routes, and resources for lemur groups to live more densely. It has already been documented that the Reserve is more densely populated with *L. catta* groups (Whitelaw and Sauther 2003). Not to be overlooked are the patches of terrestrial herbs, which will be explored in terms of diet in the coming chapter, and data in this chapter indicating how Non-Reserve habitats were significantly depauperate in this resource.

Clear differences are also apparent in the canopy connectedness between habitats. Reserve habitats are significantly more likely to have continuous cover, i.e., branches that connect (from a lemur's perspective) between trees. This variable is also connected to the significantly lower light meter readings that were measured – illustrating the abiotic affects of forest structure differences between these habitats. Other studies have indicated that increased light levels may allow for more resource production on the lower canopy and terrestrial levels of disturbed forests (Laurence et al. 2000, Lovejoy et al. 1986), however the significantly higher levels of grazing in the unprotected habitats surrounding BMSR prevent substantial undergrowth.

Tree heights were found to be significantly higher in Reserve habitats, however, crown diameter was markedly similar between Reserve and Non-Reserve habitats. Crown diameter has been shown to be closely tied to reproductive productivity in tree species. Unpublished

phenological and observational data by the BMSR ecological monitoring team provides strong evidence that the catastrophic cyclone in January of 2005 destroyed many large Reserve habitat trees bordering the Sakamena River (Jacky Youssouf, pers.comm.). These cyclonic effects have been documented clearly at other sites and it is quite possible that several habitat structure variables in this study were directly affected by the cyclone (Wright 1999, Ratsimbazafy 2006). Within the Reserve, the forest is directly adjacent to the river. With both a cyclone and accompanying flood, a large portion of the edge of the Reserve literally fell into the river, along with many old growth trees (Sauther, pers.com.). Significant lemur habitat, particularly that of Green Group, in Parcel 1 directly borders the Sakamena River (Figure 3.18). In comparison, Non-Reserve areas are buffered by large flat areas of cropland and were less affected (Figure 3.19). This destruction of tree productivity may play a role in the relative lack of differences that were found in phenological patterns between habitat types. Or, perhaps the cyclone activity evened the productivity of tree species in Reserve and Non-Reserve habitats during my study year. Comparisons between 1987-88 and 2005-06 illustrate that phenophases of several key species were different, and these disruptions may be directly linked to the cyclone of 2005. Finally, because I focused primarily on large DBH trees on my transects, which were primarily tamarind trees, this may also reflect the lack of difference in terms of large, old growth tamarind trees which dominate both Reserve and Non-Reserve habitats. As noted before, these large trees in Non-Reserve areas are difficult to cut down given their massive DBH, and are normally not removed unless local people wish to expand their crop land near the Sakamena River (Sauther, pers. comm..).

Figure 3.18 Image of Reserve habitat directly bordering the river with no protection from cyclone winds and flooding.

Figure 3.19 Image of Non-Reserve habitats with agricultural fields buffering the large, old growth tamarind trees from cyclone winds and flooding.

In terms of phenology, the same seasonal trends are evident in both habitats and there were few differences in resource availability between protected and Non-protected areas, but important differences in the availability of tamarind resources in the Reserve. The consistently large crown sizes may compensate for other disadvantages in the Non-Reserve habitats, at least for tamarind trees. Fruit resources outside the Reserve are primarily tamarind, although there are the same species available across a more dispersed and larger area. Both within and outside of the Reserve, along the Sakamena, there are similar large kily with large crown sizes. Furthermore, due to the lack of understory complexity in Non-Reserve habitats, this deficiency may allow for larger DBH trees (the focus of my phenology transects) to produce resources and reproduce at levels that are comparable to undisturbed habitats, at least in terms of tamarind. In effect, the understory deficiency allows more of the tamarinds to produce at higher levels because they are not competing with a dense array of understory species. Also, cyclone damage was more severe inside the Reserve and seems to have affected tamarind resource availability more severely inside the Reserve. Disturbed forests, in close proximity to the BMSR protected areas, may provide similar overall tamarind resource availability and could perhaps indicate a buffering effect for larger DBH tamarind trees. Resource differences are evident, however, when examining the larger amount of terrestrial herbs, number of bushes and medium bushes, and variety of foods available inside the Reserve. Notably, Ganzhorn et al. (2000b) argued that when forests are disturbed, it appears that resources can become more readily available because the canopy has opened up to let in more light and there is less competition between plants for other abiotic nutrients and resources. These variables may be key in providing animals outside of the Reserve with resources at the levels that are available inside the Reserve. However, which resource they access and their strategies to acquire these resources may present challenges to

populations that are adapted to a more stable and uniform resource base. Subsequent chapters will examine how *L. catta* groups differ in the variety of foods they consume, and behavioral strategies that allow them to accommodate different resource patterns.

One habitat that warrants a deeper observation is the Non-Reserve 3 transect. This was the third and final transect that I conducted. The quantitative results of this particular habitat indicate that it is quite similar in many respects to Reserve habitats. For instance, focal tree distance, tree height, DBH, distance to saplings and shrubs, soil compaction, and light meter reading were each more similar than the other habitats outside of the Reserve. Both Non-Reserve study groups, namely, Black and Light Blue, utilized this habitat. This habitat lies between the research camp and the Sakamena River and could prove to be a useful extension of protected habitat.

The underlying reasons that may explain differences in forest structure variables and phenological resources between the undisturbed Reserve habitats and unprotected Non-Reserve habitats are difficult to identify, but are most likely the result of three primary factors: 1.) differences existing prior to disturbance and protection; 2.) Non-anthropogenic changes induced by disturbances such as the January 2005 cyclone that may create both structural and phenological change, and; 3.) anthropogenic disturbances and their effects since the Reserve has been protected (Irwin 2006).

It has been previously noted that pre-existing changes are difficult to account for in cross-sectional studies (Irwin 2006). To control for any extraneous variables as much as possible in a cross-sectional study, it is imperative to use habitats that are similar in terms of elevation, rainfall, resource availability, and temperature variation. These habitats, Reserve and Non-Reserve, were selected for their similarities – the only difference being their protected, fenced

status. Indeed, the primary variable in this area that seems to dictate vegetative differences is distance from the Sakamena River, and these habitats were quite similar in their distance. Future studies investigating more detailed phenological data will be necessary to tease apart the resource availability in the unprotected habitats.

Along with more detailed phenological investigations, Non-anthropogenic affects, such as differential tree mortality and reproductive success need a closer examination in this region. These variables will contribute significantly to the structure and composition of these forest over time. The protection and slowing of anthropogenic effects of this region are relatively recent, and it is possible that the time scale is too short to have had a significant affect on the measurements in this study. A thorough examination of abiotic effects such as altered environmental conditions and increased windthrow remains to be seen.

A major concern for these forests is the differential reproductive success and successional processes for the future. In some disturbed areas, there are only mature trees (mainly kily) and few to no saplings present in the understory. Anthropogenic disturbance has most likely played a major role in driving these observed and marked differences in forest structure. It is extremely difficult to pinpoint extraction rates and grazing impacts without direct observations, but, key lines of evidence including lack of herbs, saplings, distance to understory specimens, and overall reduced density of species strongly implicate anthropogenic pressures (Irwin 2006, Laurance et al. 1997, 1998, 2000). Results presented here indicate that human activity such as grazing, foot traffic, and extraction have compounded the effects of natural disasters (including drought and cyclone) to create a potently unpredictable environment.

Apart from the fundamental causes of these structural and resource differences, the altered landscape, canopy, and terrestrial obstacles “lead to direct and complex challenges for

animal communities living in fragments" (Irwin 2006, p. 206). Several key and obvious resources such as sleeping requirements and locomotor pathways are seriously altered with the quantified differences assessed in this chapter. Indeed, more open canopies, more exposed terrestrial travel, diet adjustments to fit an altered resource based may have serious, and perhaps critical, effects on animals' energy balance and ability to be biologically successful.

Primates are known for their behavioral flexibility and adaptability, but few studies have examined the effects of anthropogenic disturbance on the behavioral ecology of forest dwelling primates. As a result, anthropologists and conservationists alike have collected few concrete variables dictating whether or not a species will tolerate disturbance or fail to thrive in anthropogenically altered landscapes. The following chapters will examine such effects of anthropogenically disturbed habitats on the behavior and ecology of the ring-tailed lemur in and around Beza Mahafaly Special Reserve in southwestern Madagascar.

CHAPTER 4

EFFECTS OF ANTHROPOGENICALLY ALTERED FOREST ON *LEMUR CATTA*: FEEDING ECOLOGY

4.1 Introduction

4.1.1 Anthropogenically Altered Forests: Habitat Loss and Conversion and Species Extinctions

The loss of primary primate habitat, and the accompanying destruction and conversion, has been deemed one of the chief threats to biodiversity throughout the world (Cuaròn 2000). The dominant types of loss and modification currently are related directly to human activities. Scientists argue that it is critical to understand the processes of anthropogenic habitat disturbance in order to at least mitigate, if not eliminate, the negative changes (Laurance and Bierregaard 1997). Before this, we first must understand what types of changes they evoke in wildlife species. Quantitatively, it is relatively simple and useful to monitor the overall loss of habitat through remote sensing of both the area of habitat remaining and its spatial relationship within the landscape (Green and Sussman 1990, Irwin et al. 2005). Indeed, these methods make it possible in some discrete examples to predict the loss of species by quantifying the area of habitat that has been significantly altered and is no longer ecologically viable for wildlife (Cowlishaw 1999, Ganzhorn et al. 2003). While this approach is useful in the larger picture of analyzing conversation priorities, it fails to identify which taxa may be more vulnerable or which ecological processes and feedback mechanisms are pushing some taxa to extinction (Irwin 2006). Finally, the larger scale approach also ignores how the remaining landscape configuration continues to add to biodiversity losses, a known occurrence in altered landscapes (Laurance et al. 2002).

As discussed in Chapter One, for wildlife inhabiting anthropogenically altered forests, there are several challenges that can be broadly grouped in the three categories mentioned above: proximate anthropogenic effects, degraded habitat variables and unsuitability of habitat, and the effects of landscape-level changes. Potent and dramatic are the direct effects of hunting, disease, and introduced predators on endemic populations. These are proximate factors that act quickly to eliminate individuals and may drastically reduce population size. On a longer time scale, the second category includes alterations to a habitat and its resource base. Research has shown that while it appears superficially to be less devastating than the outright denuding of forested land (i.e. fewer forested acres are converted to Non-forested land), fragmentation and degradation are more subtle and insidious (Sechrest and Brooks 2002). Furthermore, when parts, or aspects, of the natural environment are removed or altered (extractive processes), these actions impose differential mortality on the historic ecological patterns. As a consequence, the habitat is less suitable for some organisms that have evolved to the pressures of an undegraded environment. Many human processes and activities contribute to habitat degradation including heavy human or livestock usages, extraction of resources, crop irrigation, and suppression of natural fire regimes, and conversion to agriculture (Sechrest and Brooks 2002). Commonly, anthropogenic processes drive the degradation process further into habitat fragmentation. Degraded habitats and unsuitable habitat may inhibit wildlife population success or persistence, or create behavioral and ecological changes in response to changes in the habitat. The third category affecting wildlife in anthropogenically altered habitats are landscape level effects and changes. These effects act on populations in the longest time scale. They affect population viability through limiting critical processes such as dispersal, and increasing the predation risk for individuals traveling through exposed matrix habitats.

A consistent theme in the research literature examining the ability of species to persist in anthropogenically altered habitats is variability (Chiarello and de Melo 2001, Ganzhorn et al. 2000ab, Ganzhorn et al. 2003, Gilbert and Setz 2001Onderdonk and Chapman 2000, Tutin et al. 1997, Umapathy and Kumar 2000a). In the vast majority of studies, the variation is so abundant that there are no clear ecological variables such as body size, social organization, locomotor pattern, home range that can be correlated definitively to the variation in responses (some positive, some negative, and some seemingly neutral) of wildlife to habitat alterations.

Indeed, several comprehensive studies examining the probability of extinction for mammalian species assemblages in Madagascar illustrated that extinction proneness in fragments is consistent, and disturbed and fragmented landscapes are highly nested (Ganzhorn et al., 2000a,b, 2003). These authors estimated original population sizes in disturbed and fragmented habitats, based on current population densities. Results indicated that higher original population sizes tended to correlate with a greater chance of population survival and success. As previous discussions have indicated, species varied in their response to disturbance and fragmentation and this variation was not explained with the nested subset theory. This theory is an extension of the species-area relationship component of Island Biogeography Theory and its premise holds that species-poor small islands (or disturbed habitats) should support faunal assemblages that are subsets of larger islands (or continuous, undisturbed habitats) (Lindenmayer and Frank 2002). However, population density in continuous habitats may not be able to predict species extinction proneness in disturbed forests: disturbed forests' characteristics may severely change a habitat's resource base and its carrying capacity. As has been shown with primates in numerous studies, fragment area (or the area of disturbed forests) is not usually a significant indicator of species persistence in fragments and disturbed forests. For example, in Ranomafana, an in depth study

examining lemur species assemblages at Ranomafana showed the presence of nested subsets in fragments (Deghan 2003). Specifically, smaller fragments contained some of the same lemur species as were present in continuous habitats. However, neither fragment area nor lemur species' body mass, relatively simple measures of species characteristics, are predictors of lemur species richness in fragmented and disturbed habitats (Deghan 2003). Behavioral plasticity, flexibility, and quantitative measures of species requirements and resources available in altered habitats are more likely to have predictive power in altered landscapes (Irwin 2006). These more dynamic variables, while more challenging to capture, may be more significant in assessing species population persistence than more static variables such as body weight and forest fragment area.

Capturing these intricate variables of resource availability throughout seasons, feeding patterns, and forest structure requires long-term ecological study. A thorough understanding of how the effects of anthropogenic habitat alteration affect the core of populations will promote valuable conservation management practices and an understanding of population dynamics in an ecological framework. Moreover, adding to the work of primate researchers examining the obvious abundance of variation in primates ability to exist in altered habitats will eventually lend clarity to the sea of inadequate predictive power conservationists are currently equipped with. A better understanding of the effects of anthropogenically altered habitats on ring-tailed lemur feeding ecology will provide significant information for the management of this species at a landscape level, especially as it pertains to protected and unprotected habitats in the Beza Mahafaly region. Further, feeding ecology is a natural foundation to examining less resource intense behavioral ecological variables such as activity patterns, social behavior, and spatial

ecology. Finally, comparing populations with different ecological pressures and habitats, are relevant to furthering socioecological theory in general.

4.1.2 Altered habitats and primate feeding ecology

Feeding ecology is sensitive to the effects of anthropogenic habitat disturbance and its accompanying fragmentation in a number of ways. Food resources may be absent; lower in abundance and availability; if present they may be distributed differently (perhaps much more widely). These changes may necessitate dietary shifts and accompanying behavioral shifts, such as daily ranging patterns, resting patterns, and adjustments to time spent developing social relationships. Anthropogenically altered habitats may not always inhibit resource availability. For example, Ganzhorrn (1995) illustrated that lower levels of disturbance, such as selective logging, can increase both the quality (higher levels of protein, lower levels of hard to digest fiber) and density of food resources for folivores in Madagascar. Indeed, in the absence of grazing, unconnected canopies (sometimes the result of selective tree harvesting) can increase the number of terrestrial herbs (Whitelaw and Sauther 2002). More times than not, however, for primates that rely on food resources and plant species that are targeted for harvest, or cleared for agricultural fields, the availability of these resources will decrease. Subsequently, primate populations will have difficulty persisting, when travel costs grow too high to acquire the necessary energy intake, resulting in local extinctions. Because lower levels of disturbance tend to increase leaf quality and production, folivorous primates are more likely to persist in altered habitats, while frugivores are more likely to fail (Johns and Skorupa 1987). Variation within these dietary types, however, is the rule and a consistent pattern in the literature (Cowlishaw and Dunbar 2003, Irwin 2006).

While multiple studies have attempted to quantify and predict incidence patterns of primate populations in anthropogenically altered habitats, long-term studies seeking to understand primate feeding ecology and diet patterns have been few. Some studies have illustrated key differences in diets of primates in continuous versus altered habitats. Mustached gueNons (*Cercopithecus cephus*) in fragmented habitats, for example, shifted their diets to consume more insects and leaves in contrast to their continuous habitat conspecifics in the same area who consumed more fruits, seeds, and flowers (Tutin 1999). In India, lion-tailed macaques eat fewer flowers, fruit, and insects in anthropogenically altered habitats (Umapathy and Kumar 2000a). Further, they are more likely to consume cultivated and introduced species (Singh et al. 2001). Variation, however, is the consistent theme in behavioral ecology for primates and other studies have found the opposite result. For example, Onderdonk and Chapman's (2000) results illustrate that different species were eaten by black and white colobus (*Colobus guereza)* in continuous and anthropogenically altered forests, but they ate the same plant parts.

The feedback mechanisms of dietary shifts will most likely vary depending on the severity of differences between habitat and how they influence primate behavioral ecology. While some may not affect any aspect of a species behavior, impacts will most likely vary according to the degree of change and the significance of the food part or food species involved (Irwin 2006). Cascading effects of lower quality diets may impact health, leading to impacts on reproductive success, mortality of all age classes, and ability to withstand predation and disease pressures. Altered feeding ecology may translate into altered ranging patterns, group and intra-group spacing depending on resource availability. Further, daily social and activity patterns can change to accommodate a more challenging resource acquisition environment. These impacts may have consequences for population persistence and may be the underlying variables that can

predict species viability in altered landscapes, as opposed to more static variables such as overall diet categories and body mass. A thorough understanding of the effects of changes in feeding ecology among habitats is valuable as they may significantly alter the viability of populations.

4.1.3 Cyclones and Primate Feeding Ecology

As noted in previous chapters, cyclones have been suggested to play a major role in the evolutionary history of the organisms of Madagascar (Binggeli 2003, Wright 1999). Often, natural disasters can severely impact the behavioral ecology of primates, particularly frugivores (Bellingham 2008, O'Brien et al. 2003). Food resources are typically reduced after a cyclone (O'Brien et al. 2003, Pavelka and Behie 2005) and primates tend to shift their diets to less preferred items or eat only the few species and plant parts that remain, thereby narrowing their diets (Behie and Pavelka 2005, Berenstain 1086, Tsuji and Takatsuki 2008). Additionally, several studies have documented that primates have coped with post-cyclone effects by spending less time active, foraging greater distances, or decreasing travel time and distances (Berenstain 1986, Dittus 1985ab, Lugo 2008, Pavelka and Behie 2005, Tsuji and Takatsuki 2008). Primates that focus their feeding and foraging on upper canopy and emergent trees typically experience the greatest post-cyclone impacts because these trees often experience more damage than do the more protected subcanopy trees and shrubs (Dittus 1985a).

Natural disasters such as cyclones, droughts, and severe storms have been shown to affect feeding strategies of lemur populations in Madagascar (Ganzhorn 1995, Gould et al. 1999, Gould et al. 2003, Ratsimbazafy 2006, Ratsisetraina 2007, Wright 1999). For example, after a direct hit from a cyclone, *Varecia variegata* were able to diversify their diet to include more species of fruit in the forests of Manombo (Ratsimbazafy 2006). Moreover, they supplemented their diets

with fruits from bushes, instead of focusing on canopy foods. In the months preceding this study at BMSR, research there demonstrated that two Reserve *L. catta* groups utilized cultivated sweet potato (*Ipomoea batatas*) leaves and stems of the invasive terrestrial herb Mexican prickly poppy (*Argemone mexicana*) outside of their typical home ranges (LaFleur and Gould 2009). Phenological data during this study showed *Tamarindus indica* to be absent due to the devastation from Cyclone Ernest in January of 2005 (LaFleur and Gould 2009). These studies show how lemurs specifically, and primates in general, can respond in varied ways to habitat disruption.

4.1.3 *L. catta* Feeding Ecology

Wild ring-tailed lemurs have a well-studied diet from several sites in Madagascar, and has been classifed as a frugivore/folivore with an "opportunistic omnivore" status as well (Budnitz and Dainis 1975, Gould 2006, Jolly 1966, Sauther 1992, 1998, Sauther et al. 1999, Simmen et al. 2003, 2006; Soma 2006, Sussman 1974, Yamashita 2002). Adaptively, *L. catta* are able to shift their dietary focus correspondingly to the highly seasonal climate and environment of Madagascar's southwestern region (Gould 2006, Sauther 1998). In fact, during different phases of the reproductive cycle, *L. catta* females rely on key species during particularly energetically demanding stages that are flush with resources (Sauther 1998). They have been documented eating unripe and ripe fruit, young and mature leaves, flowers, seeds, dead wood, invertebrates, termite trailings, occasionally vertebrates, and have been observed engaging in geophagy (Budnitz and Dainis 1975, Gould 2006, Jolly 1966, Sauther 1992, 1998, Sauther et al. 1999, Simmen et al. 2003, 2006; Soma 2006, Sussman 1974, Yamashita 2002). Finally, the *Tamarindus indica* tree (*Tamarindus indica*) has been deemed the most important

food resource for gallery forest dwelling *L. catta* (Sauther 1998, Sauther et al. 1999, Gould 2006). This chapter will revisit this key forest member.

While fruit resources have been described as being the defining and critical dietary variable for *L. catta* population viability and survival (Jolly 2003), this opportunistic omnivore also relies heavily on leaves during the course of seasonal changes (Sauther 1992, 1998: Rasamimanana and Rafidinarive 1993, Mertl-Millhollen et al. 2003, 2006). Indeed, not only arboreal leaves, but herbaceous terrestrial plants for *L. catta* living in gallery and deciduous forest has been noted as a significant part of their diet (Sauther 1998).

mediate the challenges of dry season resource shortages with both physiological and behavioral methods. For instance, ring-tailed lemurs may decrease their metabolism during seasonal shortages (Pereira et al. 1999). They may also adjust behaviorally by traveling outside of their home ranges to access both food and water (Jolly and Pride 1999, Mertl-Millhollen et al. 2006, Sauther 1998).

L. catta reproduction is tightly connected to the dynamic seasonal changes and resource availability in the southwestern region of Madagascar. Several researchers have documented clear feeding patterns among females at both Berenty and Beza Mahafaly (Rasamimanana and Rafidinarive 1993, Sauther 1994, 1998). Research investigating the differences between male and female feeding strategies has shown that during the dry season gestation period, pregnant females fed significantly more on Non-kily flowers and fruit, while males focused on leaves (Sauther 1992, 1998). At Beza Mahafaly, nursing females tended to eat more young leaves, which may be lower in secondary compounds and higher in calcium, protein, and calories – a boon to the energetically demanding lactation period for ring-tailed lemur females (Sauther 1998). Other research sites have produced different results showing that females ate more

mature kily leaves and unripe kily fruit – high in protein (Rasamimanana and Rafidinarivo 1993).

True to the "opportunistic omnivore" reputation of this species, different research locales have demonstrated they can fluctuate in their plant parts and plant species focus depending on what is available. At Berenty, for instance, several introduced plants have become a focus for groups there. Indeed, during dry season shortages of native and traditional ring-tailed lemur foods foods, these introduced species may mediate the effects of the drastic seasonal reduction and availability of resources in this Reserve (Soma 2004).

While kily has been emphasized as having great importance in *L. catta* feeding ecology, several other species also have a role rounding out this species' dietary repertoire and have even been documented as critical resources within gallery forests habitats. These include the fruits of *Enterospermum pruinosum* (vernacular: mantsaky) and *Salvadora angustifolia* (vernacular: sasavy) (Sauther 1998, Yamashita 2002). It has been suggested that all other foods, however, are secondary to tamarind (Yamashita 2002) due to the heavy reliance during the year when other fruits are unavailable. Moreover, its asynchronous fruiting and flowering patterns is key to its availability during times of other plant species shortages (Sauther 1998). Indeed, research in gallery forests of Berenty has documented that between 35-60% of total feeding time is devoted to tamarind tree fruits and leaves (Koyama et al. 2006, Mertl-Milhollen et al. 2003). Notably, when tamarind trees have failed in their reproductive cycles due to drought and cyclones, severe population declines have been documented for several years after the stochastic event (Gould et al. 1999, 2003, Gould 2006, Jolly et al. 2002).

4.1.4 Objectives

This chapter will focus on the effects of anthropogenic habitat alterations on ring-tailed lemurs by concentrating on how differential habitat resources described in the previous chapter affect feeding ecology. While this species appears particularly flexible in terms of diet, stochastic events that alter food availability have had significant impacts on demography. Earlier chapters have shown the effects of anthropogenic habitat alterations on the structure of the forest and available resources. The following questions will be addressed:

1.) Does anthropogenic habitat change affect diet of *L. catta* in terms of plant parts consumed?

2.) Does anthropogenic habitat change affect the diet of *L. catta* in terms of plant species consumed and patterns of dietary diversity?

3.) Does anthropogenic habitat change affect the feeding ecology of *L. catta* in terms of feeding versus foraging strategies?

These are significant questions that will enhance our general understanding of the behavioral ecology of endangered species in disturbed habitats, and our specific knowledge regarding management strategies for *L. catta*. To date, little has been documented about behavior of primates in disturbed, fragmented, unprotected habitats. As such, this study offers an essential step towards the comprehensive understanding of how some primates adapt and tolerate disturbance, and some simply do not. This not only provides tangible and practical knowledge to the field of primatology, it also highlights behavioral differences in conspecific populations residing in spatially close, but ecologically disparate habitats – an important test for tenets of a variety of the tenets of socioecological theory.

4.2 Analysis

4.2.1 Data Analysis

Total sample size on which the analyses are based is almost 300 group follow days which encompass almost 800 hours of contact time. For all calculation of dietary profiles and dietary diversity, I used the full sample. For phenological data, I monitored 90 trees along a 2 kilometer transect, sampling trees in each of the four groups' home ranges. More information regarding phenological sampling can be found in Chapter 2.

To understand differences between Reserve and Non-Reserve Groups in several diet variables, I analyzed monthly medians using a Kruskal-Wallis one-way analysis of variance (ANOVA). Kruskal-Wallis tests the equality of population medians among groups. A test statistic is constructed. This test statistic is distributed a chi-square with g degrees of freedom where g is the number of groups being tested. The null and alternative hypotheses (where $median_i$ is the median of group i) are:

H_0: $median_1=median_2=\ldots=median_g$ (all groups are equal: no differences exist)

H_1: H_0 is false (All groups are not equal: differences exist)

In the cases that compare the medians of four observation groups, g will be equal to 4. In the cases that compare the medians of Reserve and Non-Reserve Groups, g will be equal to 2. I used this Non-parametric test to be conservative in accepting significant results and many of these variables were not distributed normally (Siegel and Castellan 1988). Data are shown in tables and box plots. Box plots are useful to visualize the median of each group (the middle line of the plot), the next two regions surrounding the median represent the middle 50% of the data, the upper box is the 75 percentile, and the lower box is the 25 percentile of data. Finally, the upper and lower lines of the box are the maximum and minimum data points.

I assessed the groups' diet diversity for the entire study period using Simpson's diversity index:

$$D = \frac{1}{\sum_{i=1}^{s} P_i^2}$$

where S = the total number of species in the diet, and P_i = the proportion of feeding time accounted for species i. This value depends on both the overall species richness of the diet (S) and the equitability of those species. Specifically, rarely-eaten species contribute less to D than do more often eaten species. D varies between 1 and S. Values that are higher, indicate a greater diversity in that groups' diet.

4.3 Dietary Profiles: Plant Parts Consumed

4.3.1 Plant Parts Consumed: Overall Diet Consumption

Monthly and overall dietary profiles were constructed for each of the four study groups in terms of the number of instances an individual devoted to each of the various types of food items. Figure 4.1 a, b, and c illustrates the percentages based on the frequencies of plant parts consumed for each group, Reserve vs. Non-Reserve, and overall composition. The first results will examine the overall diet composition for the four groups. For each analysis, I examined differences between all four groups; Reserve vs. Non-Reserve Groups; males in all four groups; males in Reserve vs. Non-Reserve Groups; females in all four groups; and females in Reserve vs. Non-Reserve Groups.

Figure 4.1a

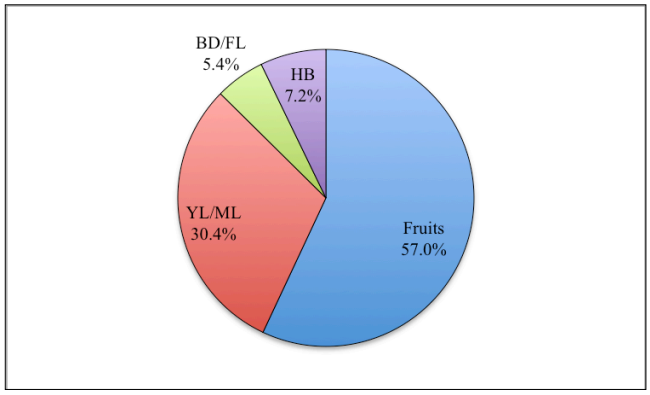

Figure 4.1a, b, and c Illustrates percentages based on the frequencies of the plant parts consumed for each group, Reserve vs. Non-Reserve, and all Groups combined. HB = herbs; BD/FL = flowers; YL/ML = leaves.

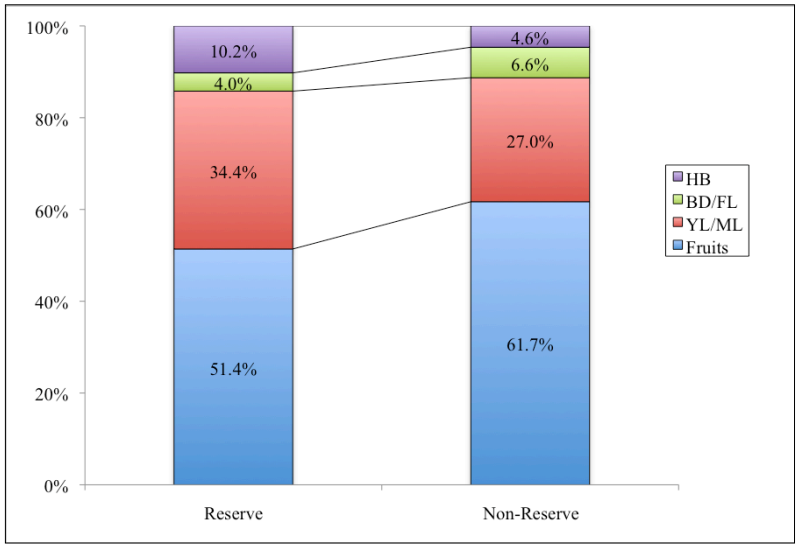

Figure 4.1b

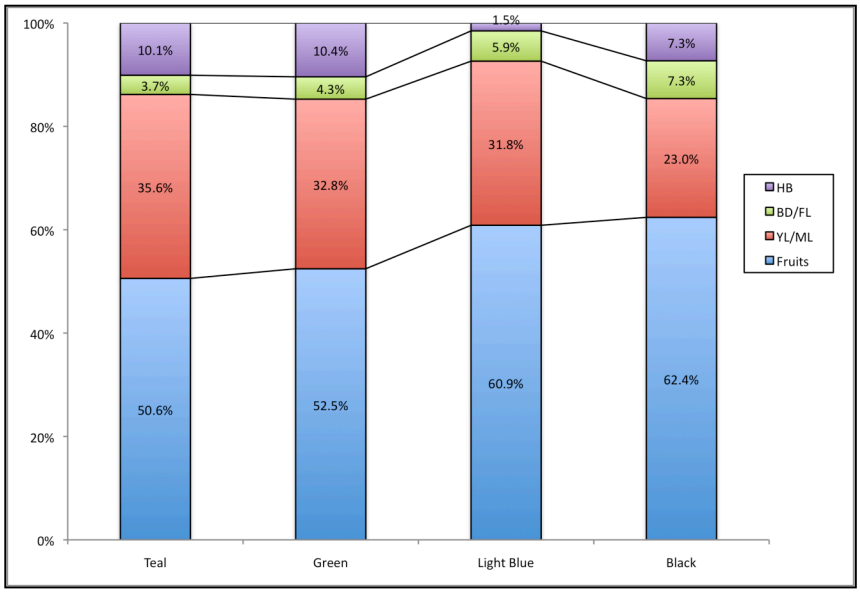

Figure 4.1c

When dietary profiles of the four study groups in BMSR are compared, several differences emerge. Specifically, several groups show differences in fruit and leaf consumption. The leaf consumption is directly related to terrestrial herbs playing an important role in several groups' diets. Notably, Black Group (Non-Reserve) consumed significantly more fruit than each of the other groups ($p<.05$) (Table 4.1).

Table 4.1 Results of fruit consumption for comparisons between each of the four study groups.

Fruit consumption comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	6.943	0.0084	Y	Y
Black vs. Light Blue	10.017	0.0016	Y	Y
Black vs. Teal	5.227	0.0222	N	Y
Green vs. Light Blue	1.502	0.2204	N	N
Green vs. Teal	0.025	0.8738	N	N
Light Blue vs. Teal	0.323	0.5697	N	N

Examining leaf consumption between the four groups illustrates an interesting pattern. Groups within the Reserve (Green and Teal) and the Non-Reserve Group closest to the Reserve (Black) each consumed significantly more leaves than Light Blue Group – the group furthest from the Reserve ($p<.05$) (Table 4.2).

Table 4.2 Results of leaf consumption for comparisons between each of the four study groups.

Leaf consumption comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.021	0.8836	N	N
Black vs. Light Blue	9.401	0.0022	Y	Y
Black vs. Teal	0.167	0.6831	N	N
Green vs. Light Blue	6.007	0.0142	N	Y
Green vs. Teal	0.000	1.000	N	N
Light Blue vs. Teal	7.293	0.0069	Y	Y

Similarly, the closest Non-Reserve Group to the protected Reserve, Black Group, consumed significantly more herbs than Light Blue Group – the group furthest to the south of the Reserve ($p<.05$) (Table 4.3). The two Reserve Groups consumed a similar amount of herbs. Green Group (the group residing closest to the river), however, was the only Reserve Group to consume more herbs than Light Blue Group. In fact, Black Group also consumed more herbs than Light Blue Group. From these results, it appears there are more differences between Light Blue Group and Green and Black. Moreover, because of Black Group's location close to the protected Reserve, there may be some buffering affects present. Finally, there were no differences between the groups for flower consumption (Table 4.4).

Table 4.3 Results of herb consumption for comparisons between each of the four study groups.

Terrestrial Herb consumption comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.002	0.9611	N	N
Black vs. Light Blue	15.652	0.0001	Y	Y
Black vs. Teal	0.135	0.7133	N	N
Green vs. Light Blue	9.779	0.0018	Y	Y
Green vs. Teal	0.045	0.8323	N	N
Light Blue vs. Teal	2.672	0.1021	N	N

Table 4.4 Results of comparison of median flower consumption for all four groups.

Flower consumption comparison between all four groups	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% significance level?	Reject H_0 at 5% significance level?
Black vs. Green	3.648	0.3020	N	N
Black vs. Light Blue	0.246	0.5143	N	N
Black vs. Teal	0.167	0.6831	N	N
Green vs. Light Blue	3.672	0.2041	N	N
Green vs. Teal	0.000	1.000	N	N
Light Blue vs. Teal	0.176	0.9833	N	N

4.3.2 Plant Parts Consumed: Monthly Variation

Monthly diet profiles for the four study groups indicate strong seasonal variation in the composition of each groups' diet (Figure 4.2 a-d). Each group consumed primarily fruit from January – June (summer and fall). Flowers and flower buds became increasingly important from March - May (fall) for each group. In the early months of the study (October/November – late spring), fruit consumption was quite low and leaves (young leaves, mature leaves) were a major component of each group's diet. Several groups also incorporate herbs at this time.

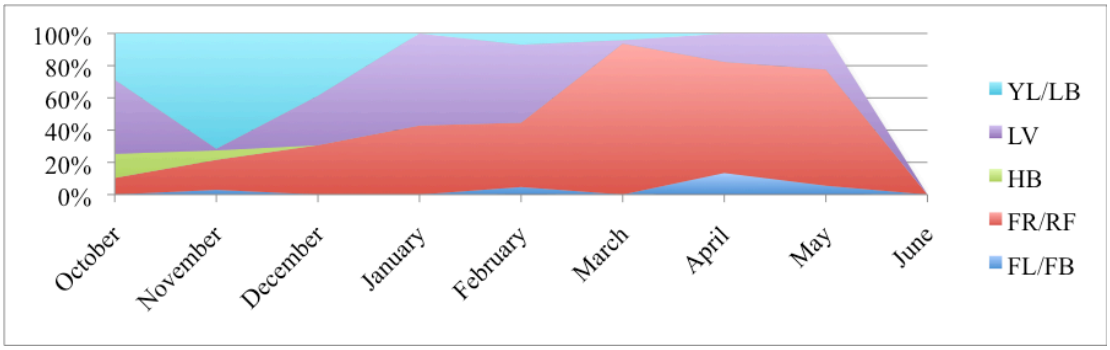

Figure 4.2a Green Group: monthly variation in detary profile (measured by percentage feeding time).

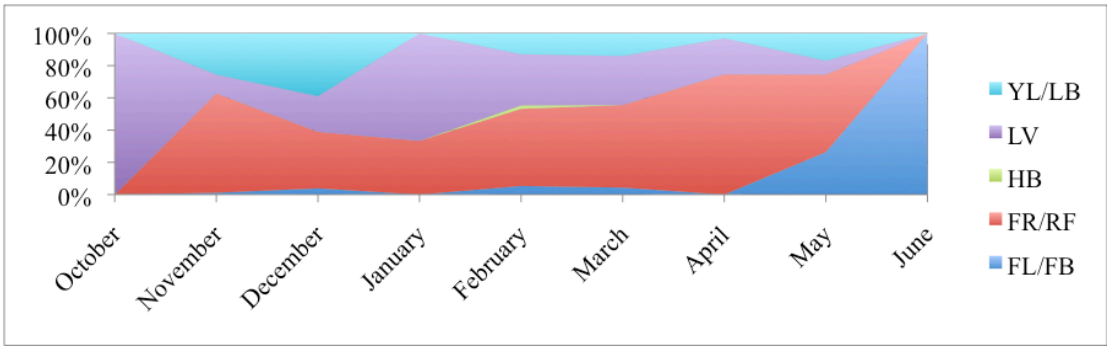

Figure 4.2b Teal Group: monthly variation in detary profile (measured by percentage feeding time).

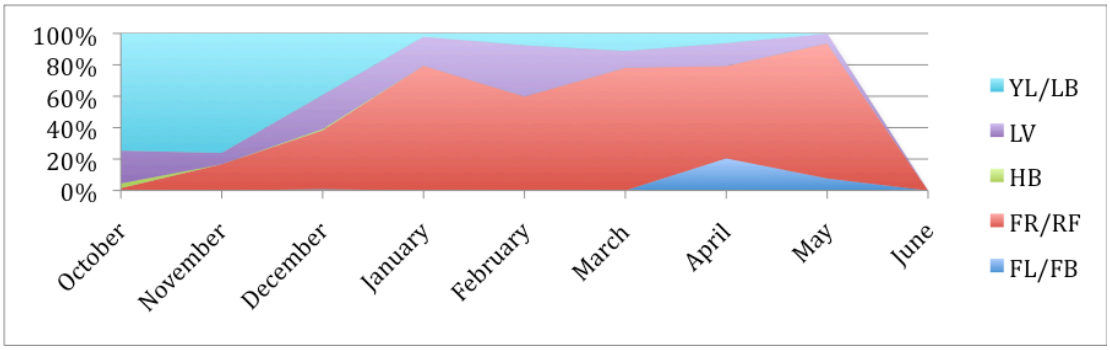

Figure 4.2c Light Blue Group: monthly variation in detary profile (measured by percentage feeding time).

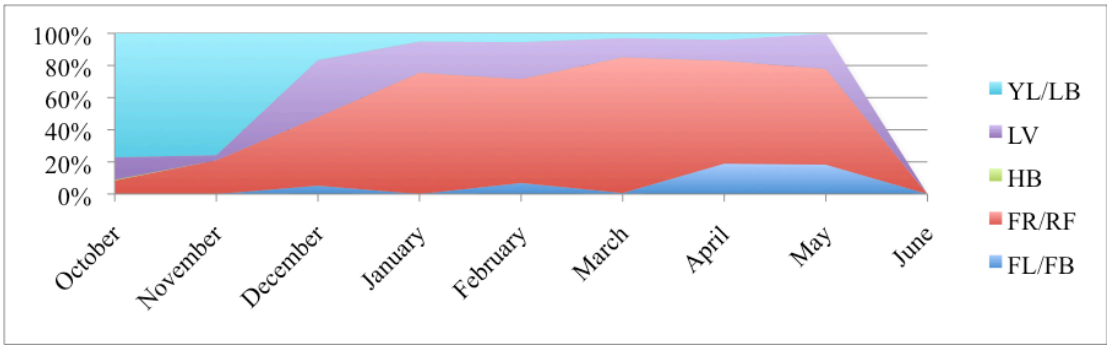

Figure 4.2d Black Group: monthly variation in detary profile (measured by percentage feeding time).

Examining the charts above indicates some minor differences in the patterns of plant part consumption. Monthly plant part consumption is closely related for both Black and Light Blue Groups. In these Non-Reserve Groups, there are some minor fluctuations in the beginning of flower consumption, the peaks and troughs of plant parts coincide remarkably similarly. On the other hand, groups inside the Reserve (Green and Teal) showed marked variation in when these individuals rely on different plant parts. Reserve Groups are both different from each other, and from Non-Reserve Groups.

Groups in anthropogenically disturbed habitats maintain a steady fruit consumption that declines in the winter months (mid-June through September) and rises steadily starting in October. In contrast, groups within the Reserve appear to have other resources that they utilize. Reserve Groups appear not to focus exclusively on fruit or young leaves; instead they tend to

ingest a wider variety plant parts. Also for Reserve Groups, mature leaves (comprised mainly of vine leaves) are a larger part of the diet in October and November. This result indicates that Reserve Groups are eating more liana, or vine, leaves and fewer young leaves in trees. .

When monthly medians are compared between these groups, several differences appear that quantify the variation seen in the above figures. As the study began in the dry months of October and November and into the rainy reason in December, there were very few significant differences between plant part consumption in the groups (Tables 4.5, 4.6). In fact, it appears that only Black Group began focusing on young leaves in the month of October while other groups relied on other plant parts (Figure 4.3) (Table 4.5). At the height of the rainy season in January, the Non-Reserve Groups, Black and Light Blue, consumed significantly more fruits than both Green and Teal Groups ($p<0.01$) (Figure 4.4) (Table 4.7). There were no other significant differences in plant part consumption in January when each group was compared.

Table 4.5 Results from Kruskal-Wallis test comparisons between all four study groups. Significant results are highlighted in yellow. B = Black, G = Green, LB = Light Blue, T = Teal.

Comparing All Four Study Groups	Value of K-Wallis Test Statistic	P-Value	Reject H_0 at 1% significance level?	Reject H_0 at 5% significance level?
October				
Fruit	0.976	0.807	N	N
Young Leaf or Leaf Bud	10.639	0.014	N	Y (B>G,LB)
Leaf	2.577	0.462	N	N
Flower	0.241	0.971	N	N
Herbs	1.107	0.775	N	N
November				
Fruit	2.433	0.488	N	N
Young Leaf or Leaf Bud	3.232	0.357	N	N
Leaf	1.268	0.737	N	N
Flower	3.787	0.286	N	N
Herbs	2.872	0.412	N	N
December				
Fruit	3.461	0.326	N	N

Young Leaf or Leaf Bud	5.732	0.125	N	N
Leaf	0.128	0.988	N	N
Flower	3.782	0.286	N	N
Herbs	5.719	0.126	N	N
January				
Fruit	25.000	0.000	Y	Y (B>G, T; LB>G,T)
Young Leaf or Leaf Bud	5.346	0.148	N	N
Leaf	5.958	0.114	N	N
Flower	0.371	0.946	N	N
Herbs	0.643	0.886	N	N
February				
Fruit	7.439	0.059	N	N
Young Leaf or Leaf Bud	1.127	0.771	N	N
Leaf	6.990	0.072	N	N
Flower	5.482	0.140	N	N
Herbs	0.241	0.931	N	N
March				
Fruit	12.372	0.006	Y	Y (B>G,T; T>LB; G>LB)
Young Leaf or Leaf Bud	1.045	0.790	N	N
Leaf	12.131	0.007	Y	Y
Flower	0.333	0.954	N	N
Herbs	0.000	1.000	N	N
April				
Fruit	5.630	0.131	N	N
Young Leaf or Leaf Bud	4.135	0.247	N	N
Leaf	2.697	0.441	N	N
Flower	9.916	0.019	N	Y(B,LB>G,T)
Herbs	0.000	1.000	N	N
May				
Fruit	9.942	0.019	N	Y (B>G)
Young Leaf or Leaf Bud	0.000	1.000	N	N
Leaf	18.620	0.000	Y	Y (B>G,T; G>LB; LB>T)
Flower	5.752	0.124	N	N

Herbs	0.000	1.000	N	N
June				
Fruit	17.803	0.001	Y	Y (B>G,T,LB)
Young Leaf or Leaf Bud	0.000	1.000	N	N
Leaf	8.495	0.037	N	Y (B>G,T;G,T>LB)
Flower	0.963	0.810	N	N
Herbs	0.000	1.000	N	N

Table 4.6 Results from Kruskal-Wallis test comparisons between Reserve and Non-Reserve Group data pooled. Significant results are highlighted in yellow. B = Black, G = Green, LB = Light Blue, T = Teal. *indicates that this comparison will not be used since there were no significant differences in the individual group comparisons.

Comparing Reserve and Non-Reserve Pooled Data	Value of Test Statistic	P-Value	Reject H_0 at 1% significance level?	Reject H_0 at 5% significance level?
October				
Fruit	0.215	0.6429	N	N
Young Leaf or Leaf Bud	2.270	0.1319	N	N
Leaf	1.305	0.2533	N	N
Flower	0.099	0.7531	N	N
Herbs	0.027	0.8685	N	N
November				
Fruit	1.088	0.2969	N	N
Young Leaf or Leaf Bud Consumption	0.954	0.3286	N	N
Leaf	0.185	0.6669	N	N
Flower	2.633	0.1047	N	N
Herbs	1.054	0.3046	N	N
December				
Fruit	3.138	0.0765	N	N
Young Leaf or Leaf Bud	0.954	0.3286	N	N
Leaf	0.007	0.9340	N	N
Flower	0.018	0.8946	N	N
Herbs	0.355	0.5511	N	N
January				
Fruit	23.856	0.0001	Y	Y (NR>R)
Young Leaf or Leaf Bud	4.491	0.0341	N	Y (R>NR) *

Leaf	4.776	0.0289	N	Y (R>NR) *
Flower	0.200	0.6549	N	N
Herbs	0.632	0.4268	N	N
February				
Fruit	3.257	0.0711	N	N
Young Leaf or Leaf Bud	0.355	0.5511	N	N
Leaf	2.741	0.0978	N	N
Flower	1.231	0.2673	N	N
Herbs	0.099	0.7531	N	N
March				
Fruit	0.355	0.5511	N	N
Young Leaf or Leaf Bud	0.799	0.3713	N	N
Leaf	0.231	0.6311	N	N
Flower	0.070	0.7911	N	N
Herbs	0.000	1.0000	N	N
April				
Fruit	0.658	0.4172	N	N
Young Leaf or Leaf Bud	3.947	0.0469	N	Y (R>NR)*
Leaf	1.799	0.1799	N	N
Flower	7.645	0.0057	Y*	Y (NR>R)*
Herbs	0.000	1.0000	N	N
May				
Fruit	0.658	0.4172	N	N
Young Leaf or Leaf Bud	0.000	1.0000	N	N
Leaf	0.046	0.8296	N	N
Flower	1.382	0.2398	N	N
Herbs	0.000	1.0000	N	N
June				
Fruit	4.283	0.0385	N	Y (NR>R)*
Young Leaf or Leaf Bud	0.000	1.0000	N	N
Leaf	1.542	0.2143	N	N
Flower	0.396	0.5292	N	N
Herbs	0.000	1.0000	N	N

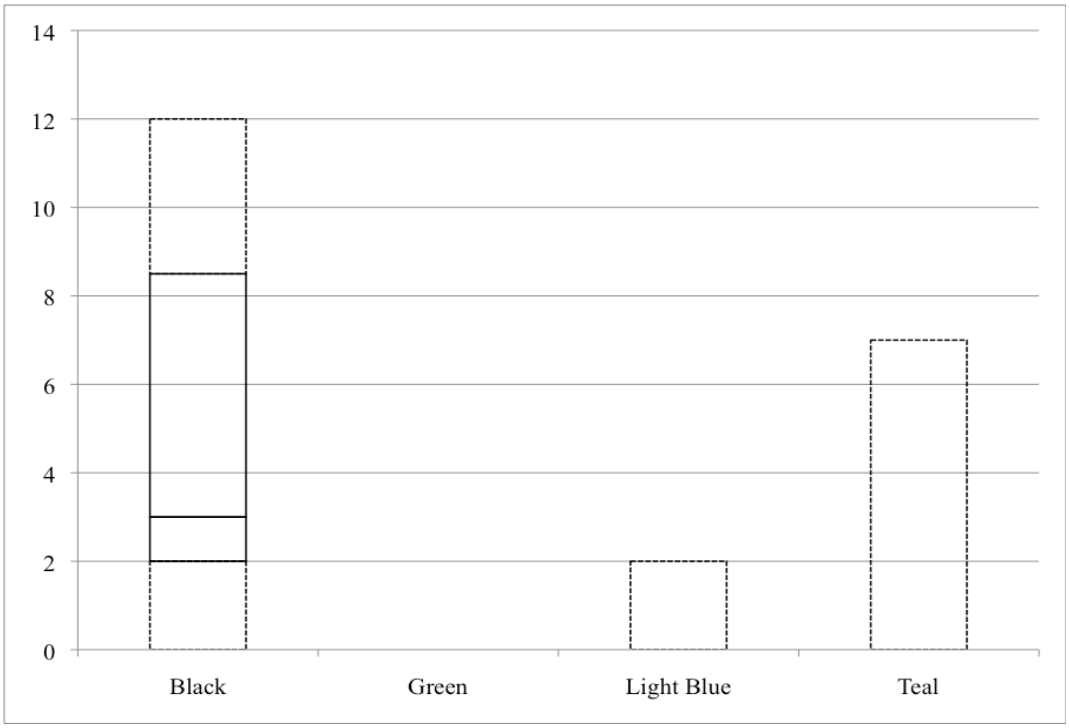

Figure 4.3 Box plot indicating median differences of young leaf consumption in October for all four study groups. Y-axis is the frequency of consumption.

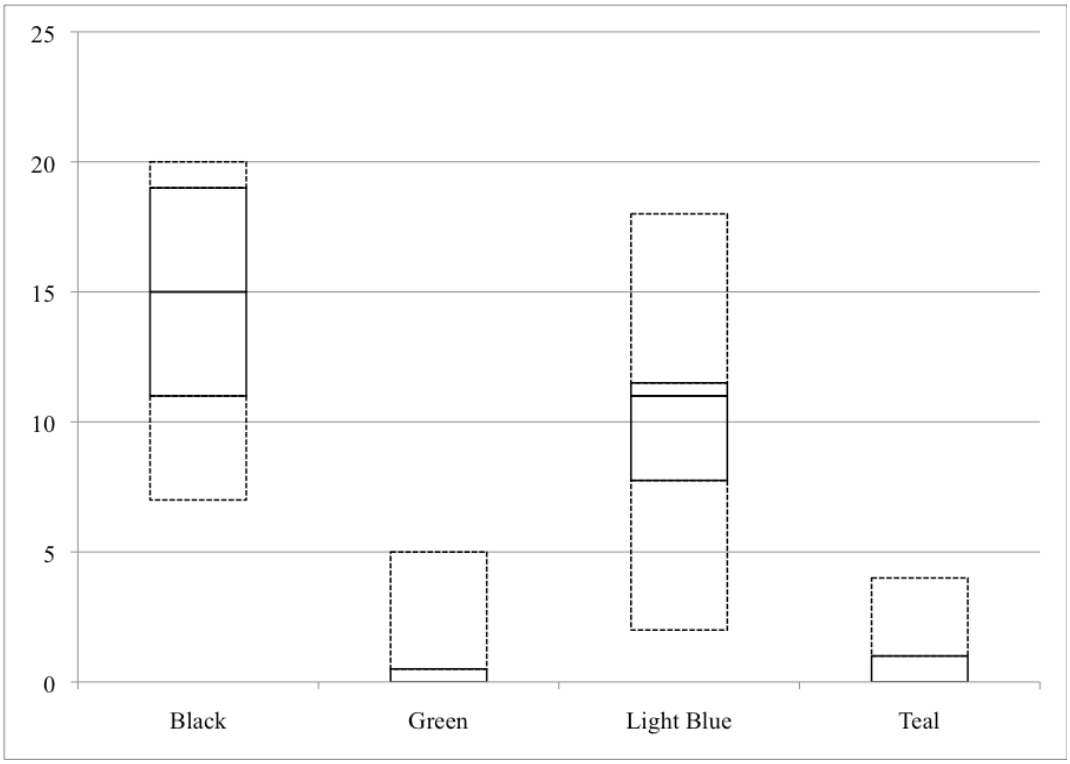

Figure 4.4 Box plot indicating median differences of fruit consumption in January for all four study groups. Y-axis is the frequency of consumption.

Table 4.7 Results of comparisons between medians of fruit consumption between the four study groups in January 2006.

Group Comparisons	Value of K-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.8	0.0017	Y	Y
Black vs. Light Blue	3.15	0.0759	N	N
Black vs. Teal	11.118	0.0009	Y	Y
Green vs. Light Blue	11.429	0.0007	Y	Y
Green vs. Teal	0.179	0.672	N	N
Light Blue vs. Teal	13.395	0.0003	Y	Y

As the rainy season continued in February, there were no significant differences in plant part consumption between the study groups (Table 4.5). During the last wet month of the austral summer, Black Group relied on leaves significantly more than both Green and Light Blue Groups and more on fruit than both Green and Teal Groups (Figures 4.5, 4.6) (Tables 4.9, 4.10). Light Blue Group consumed the lowest number of fruit parts, significantly less than both Green and Light Blue (Figure 4.5).

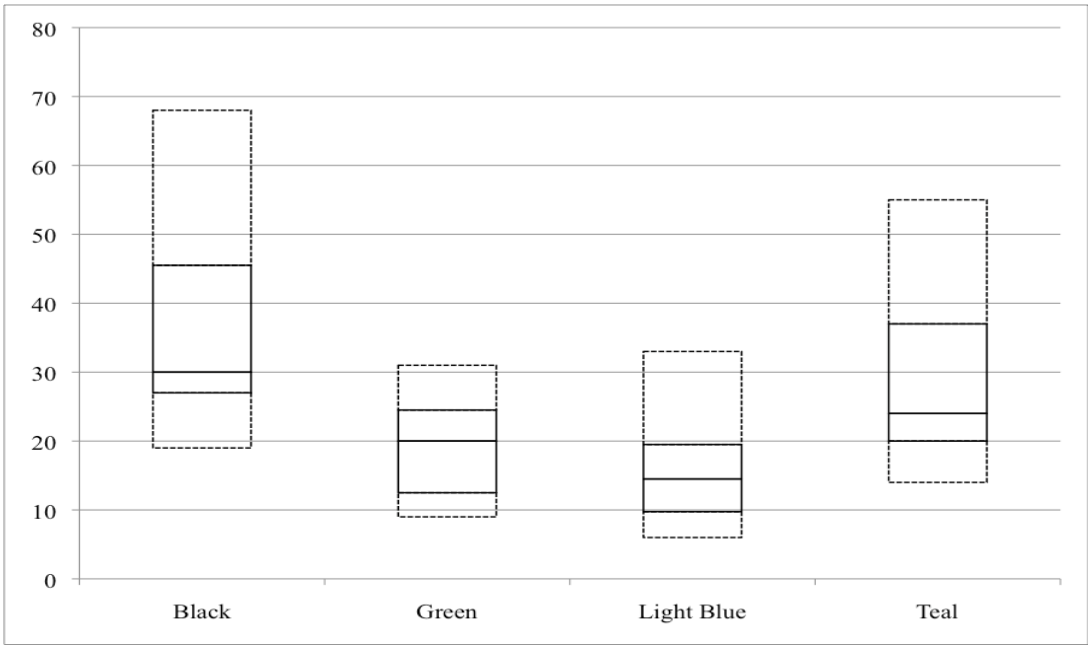

Figure 4.5 Box plot indicating median differences of fruit consumption in March for all study groups. Y-axis is the frequency of consumption.

Table 4.8 Results of comparisons between medians of fruit consumption between the four study groups in March 2006.

Test	Value of Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	4.445	0.0350	Y	Y
Black vs. Light Blue	8.257	0.0041	N	N
Black vs. Teal	1.356	0.2443	Y	Y
Green vs. Light Blue	0.714	0.3980	Y	Y
Green vs. Teal	2.356	0.1248	N	N
Light Blue vs. Teal	6.365	0.0116	Y	Y

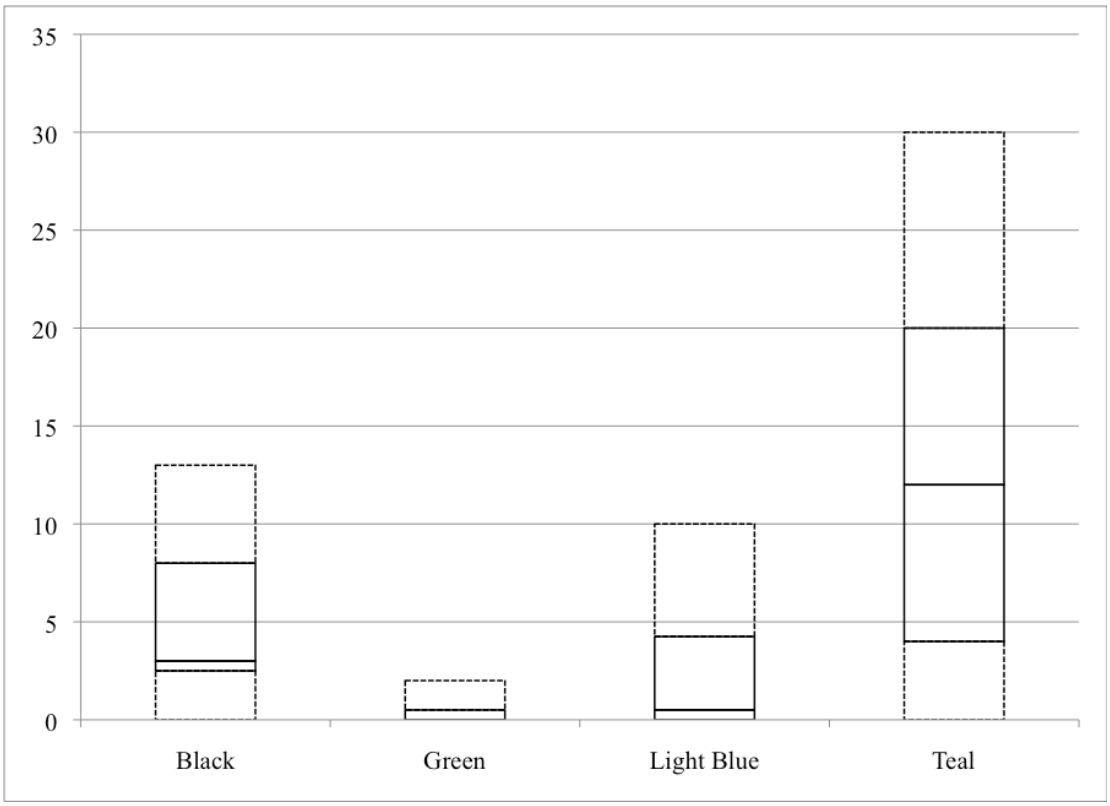

Figure 4.6 Box plot indicating median differences of leaf consumption in March for all study groups. Y-axis is the frequency of consumption.

Table 4.9 Results of comparisons between medians of leaf consumption between the four study groups in March 2006.

Test	Value of Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	6.208	0.0127	N	Y
Black vs. Light Blue	1.945	0.1632	N	Y
Black vs. Teal	1.894	0.1688	N	N
Green vs. Light Blue	1.302	0.2539	N	N
Green vs. Teal	7.286	0.0070	N	N
Light Blue vs. Teal	6.011	0.0142	N	N

As the dry season resumes in the months of April, May, and June groups show minor differences in plant part consumption (Table 4.5). In April, both Black and Light Blue Group relied significantly more on flowers than the both Green and Teal when groups were compared individually (Figure 4.8) (Table 4.10). This difference is also significant when Non-Reserve and Reserve Group data are pooled together (Figure 4.9) (Table 4.10).

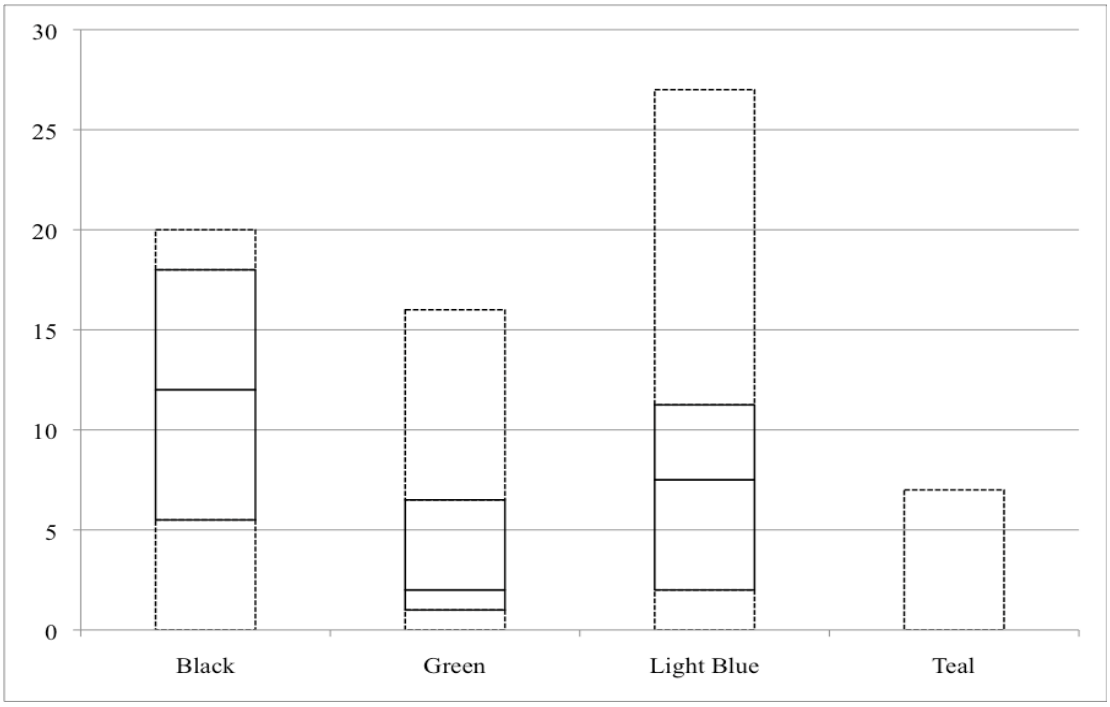

Figure 4.8 Box plot indicating median differences of flower consumption in April for all study groups. Y-axis is the frequency of consumption.

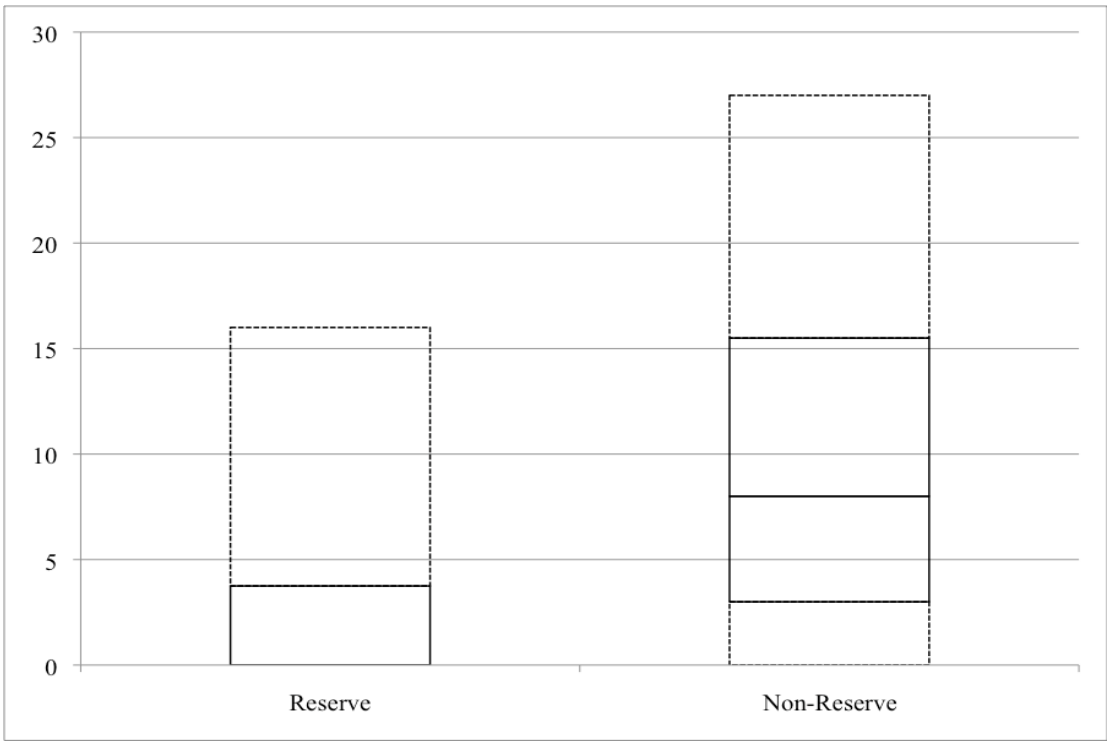

Figure 4.9 Box plot indicating median differences of flower consumption in April for Non-Reserve and Reserve pooled data. Y-axis is the frequency of consumption.

Table 4.10 Results of comparisons between medians of flower consumption between the four study groups, and the pooled data comparisons from April 2006.

Comparison of all four study groups	**Value of K-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	2.976	0.0245	Y	Y
Black vs. Light Blue	0.864	0.3525	N	N
Black vs. Teal	5.672	0.0172	Y	Y
Green vs. Light Blue	0.864	0.3525	Y	Y
Green vs. Teal	2.356	0.1248	N	N
Light Blue vs. Teal	6.729	0.0095	Y	Y
Comparison of Non-Reserve and Reserve Groups' pooled data	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Flower Consumption	7.645	0.0057	Y	Y

Resource consumption comparisons in both May and June show that there are a few significant differences (Figures 4.10, 4.11,4.12; Tables 4.11, 4.12, 4.13). For example, in May, Black consumed significantly more leaves than both of the Reserve Groups, however Light Blue Group consumed fewer than Green but more than Teal (Figure 4.10). In June, Black Group consumed far more fruit and more leaves than each of the other groups (Figure 4.11, 4.12; Table 4.12, 4.13).

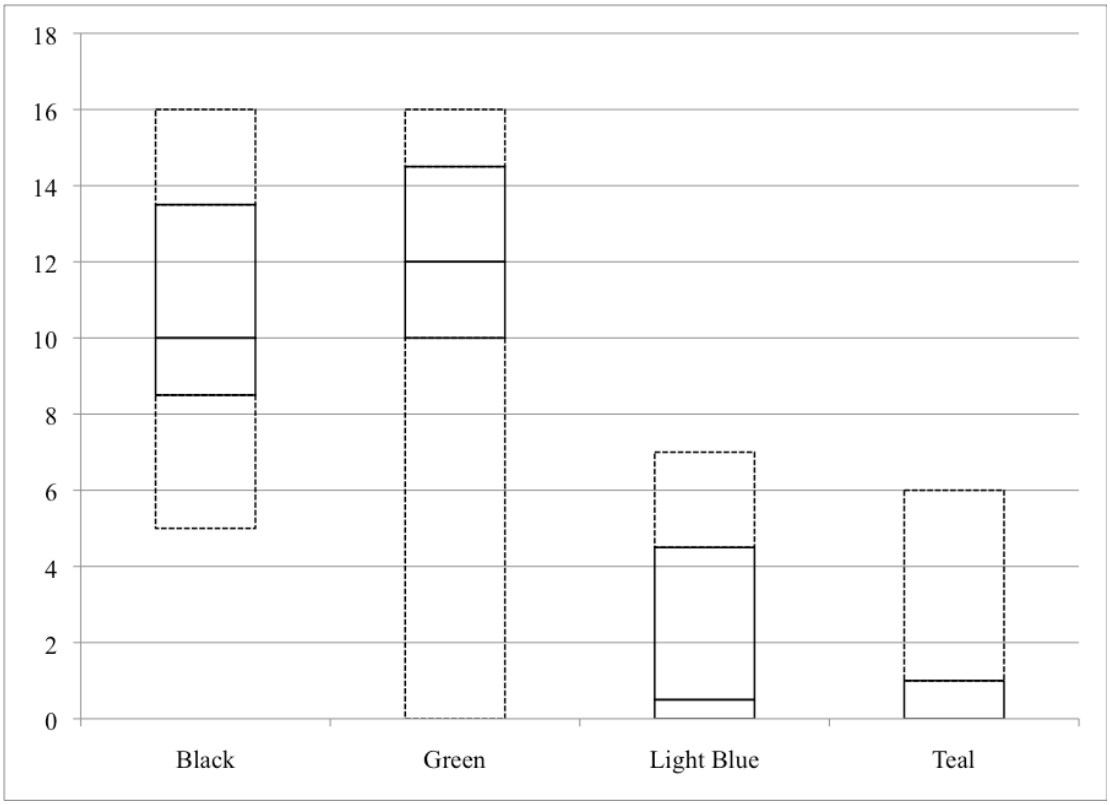

Figure 4.10 Box plot indicating median differences of leaf consumption in May for all groups. Y-axis is the frequency of consumption.

Table 4.11 Results of comparisons between medians of leaf consumption between the four study groups from May 2006.

Comparison of all four study groups	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.102	0.7494	Y	Y
Black vs. Light Blue	10.314	0.0013	N	N
Black vs. Teal	10.423	0.0012	Y	Y
Green vs. Light Blue	7.779	0.0053	Y	Y
Green vs. Teal	7.286	0.0070	N	N
Light Blue vs. Teal	0.668	0.4138	Y	Y

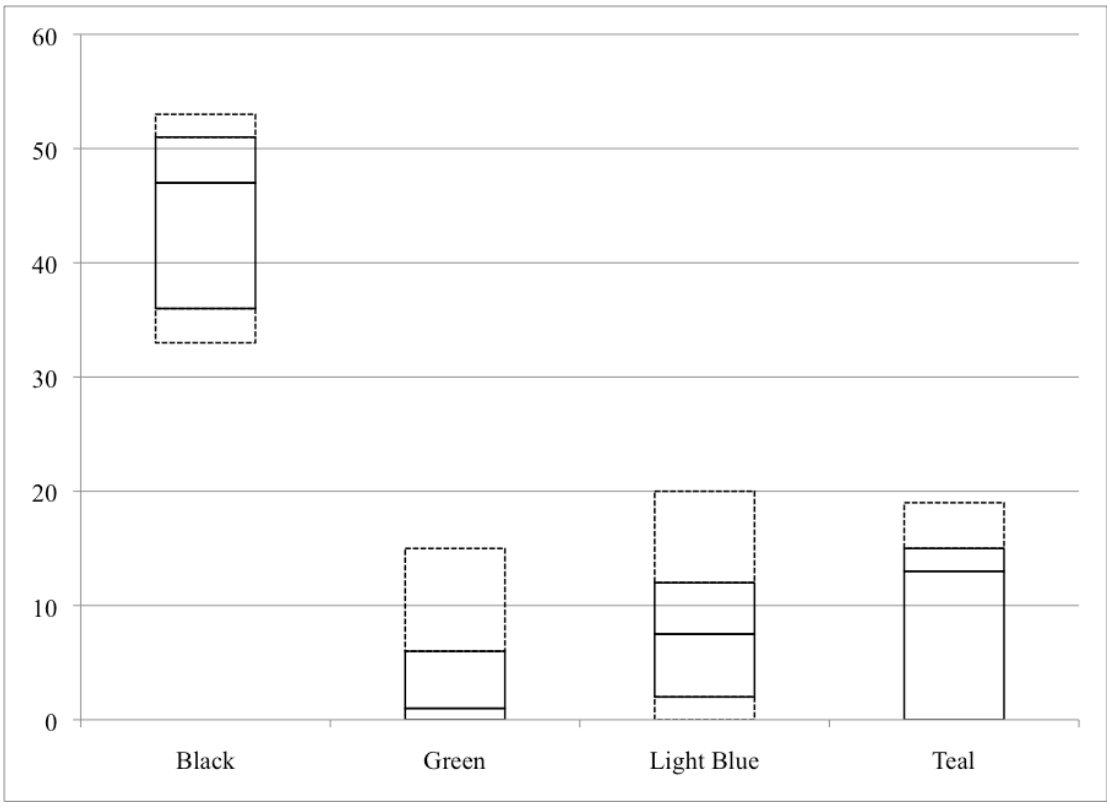

Figure 4.11 Box plot indicating median differences of fruit consumption in June for all groups. Y-axis is the frequency of consumption.

Table 4.12 Results of comparisons between medians of fruit consumption between the four study groups from June 2006.

Comparison of all four study groups	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.800	0.0017	Y	Y
Black vs. Light Blue	12.600	0.0004	Y	Y
Black vs. Teal	11.118	0.0009	Y	Y
Green vs. Light Blue	1.829	0.1763	N	N
Green vs. Teal	1.356	0.2443	N	N
Light Blue vs. Teal	0.456	0.4996	N	N

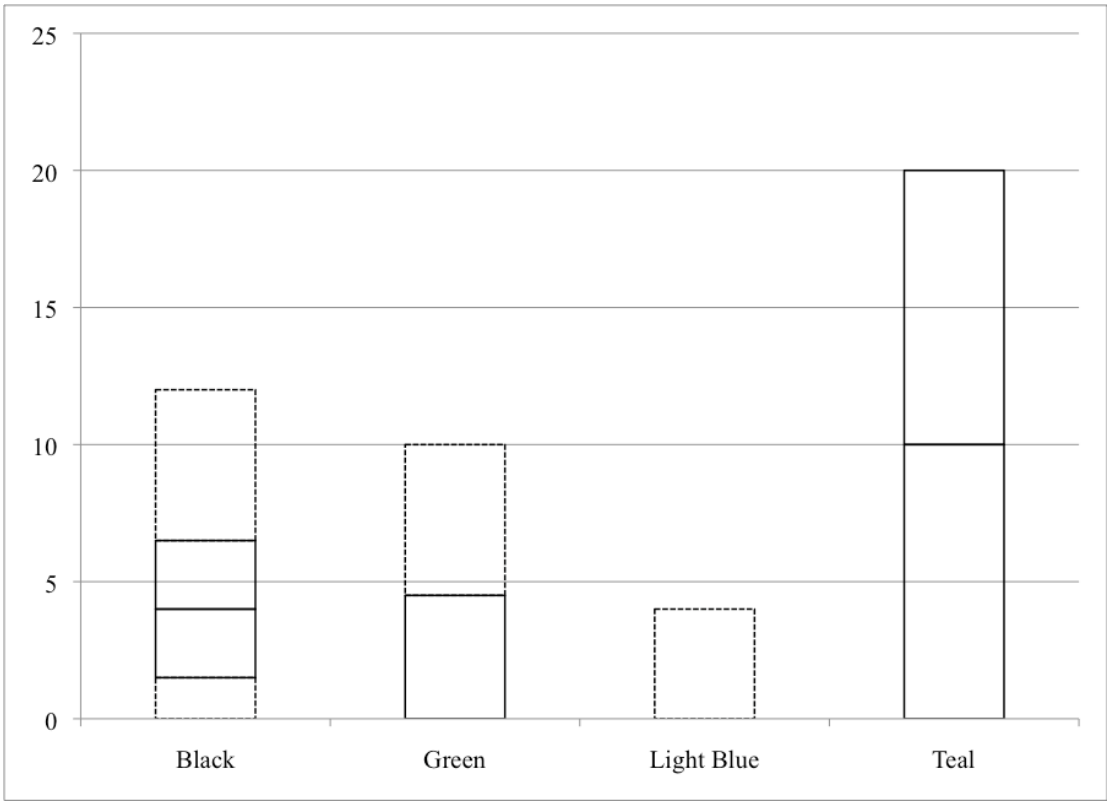

Figure 4.12 Box plot indicating median differences of leaf consumption in June for all groups. Y-axis is the frequency of consumption.

Table 4.13 Results of comparisons between medians of leaf consumption between the four study groups from June 2006.

Comparison of all four study groups	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	1.322	0.2502	Y	Y
Black vs. Light Blue	7.779	0.0053	N	N
Black vs. Teal	0.137	0.7110	Y	Y
Green vs. Light Blue	1.607	0.2049	Y	Y
Green vs. Teal	1.235	0.2664	N	N
Light Blue vs. Teal	3.960	0.0466	Y	Y

4.4 Dietary Profiles: Taxonomic Composition of Diet

4.4.1 Taxonomic Composition of Diet: Overall Diet Composition

Similar to the differences between groups in terms of plant parts consumed, there are also differences among the groups in the plant species from which the diet is composed. This is not entirely surprising given the habitat differences addressed in Chapter 3. See figures below of the top 13 species (species that make up greater than 1% of the diet) consumed by each of the four study groups, Reserve and Non-Reserve Groups combined, and all four study groups combined (Figure 4.13 a,b,c):

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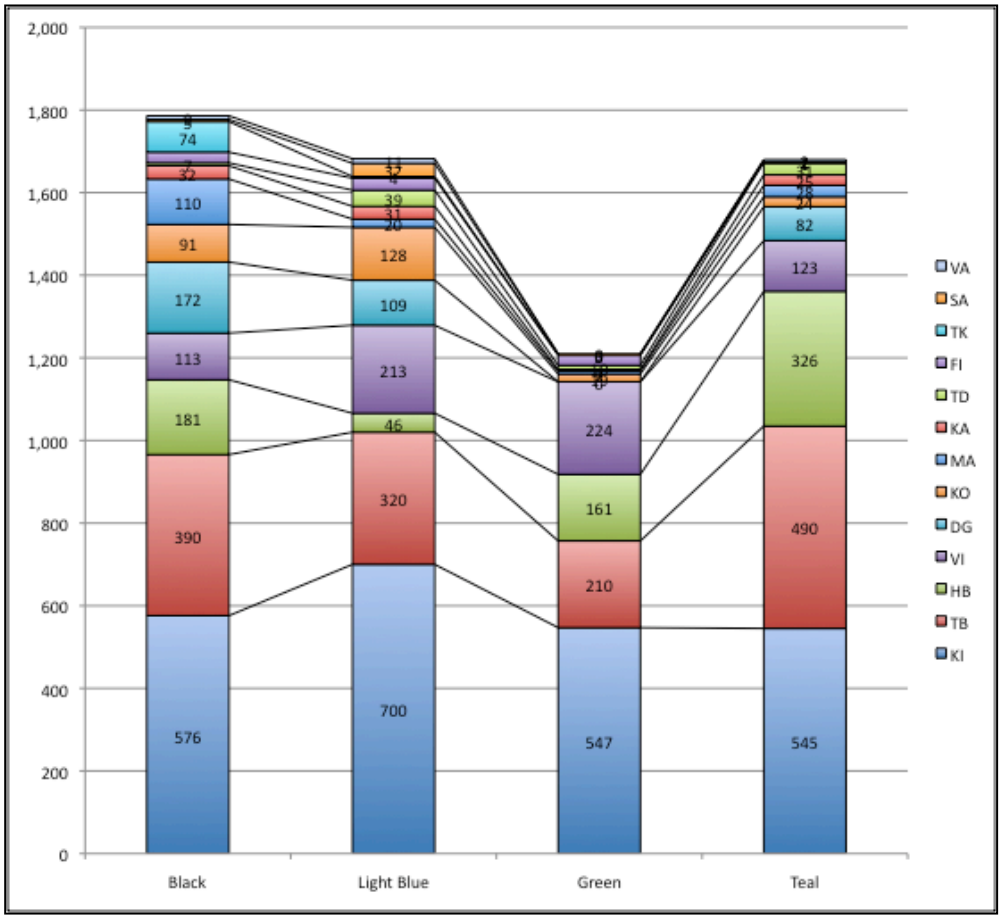


Figure 4.13a Comparison of each groups' species consumption. X-axis indicates the number of times each species was eaten.

Species Code	**Malagasy Name/Species Name**
KI	Kily – *Tamarindus indica*
TB	Tratraborondreo - *Grewia leucophylla*
HB	Terrestrial Herb-*Metaporana parvifolia*
VI	Liana vine - *Boerhavia diffusa*
DG	Dango - *Tallinella grevei*
KO	Kotipoke - *Grewia grevei*
MA	Mantsaky - *Enterospermum pruinosum*
KA	Katrafay - *Cedrelopsis grevei*
TD	Tainkafotse - *Grewia franciscana*
FI	Filo filo - *Azima tetracantha*
TK	Tsikidrakatse – *Bridelia* sp
SA	Sasavy - *Salvadora angustifolia*
VA	Valiandro – *Quivisianthe papinae*

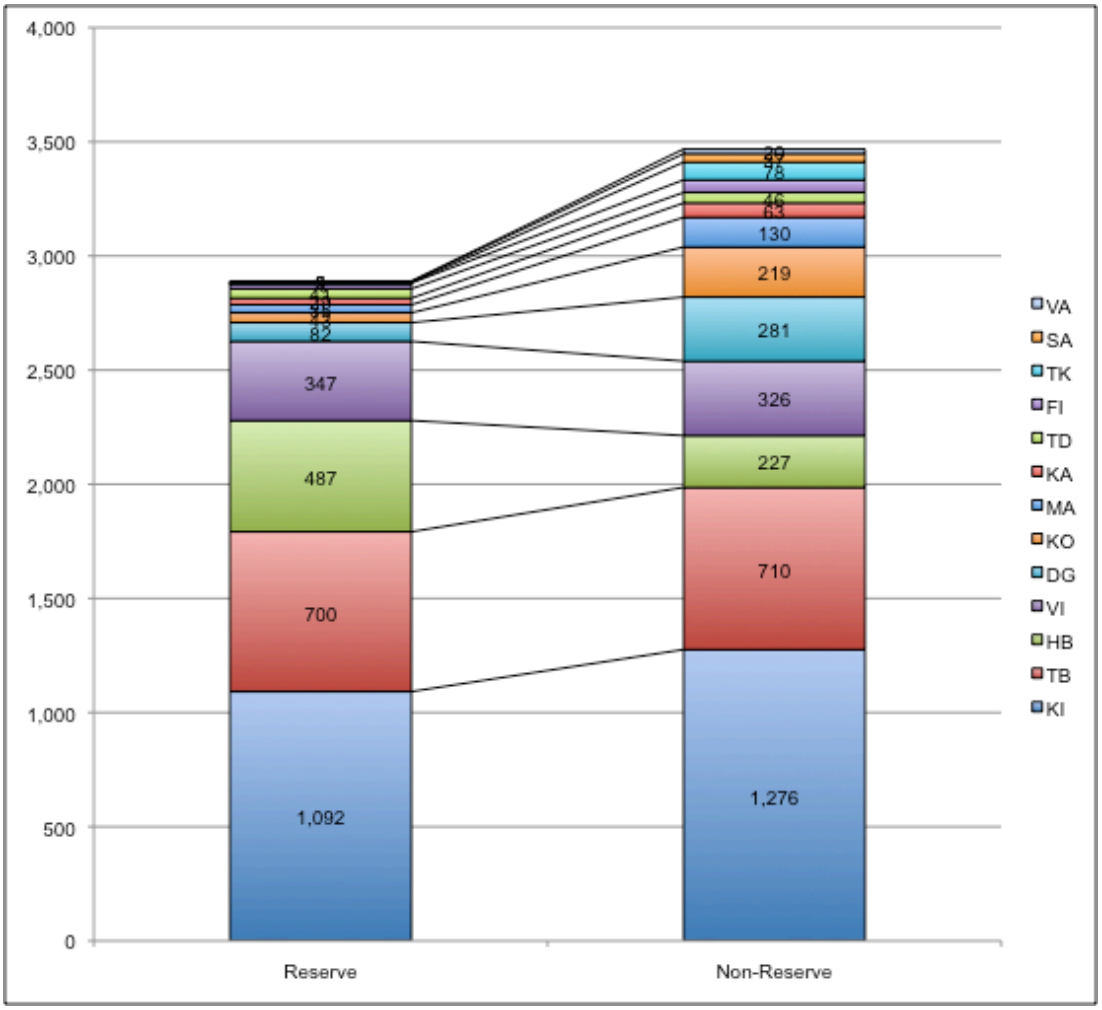


Figure 4.13b Overall comparison of Reserve vs. Non-Reserve Groups' species consumption.

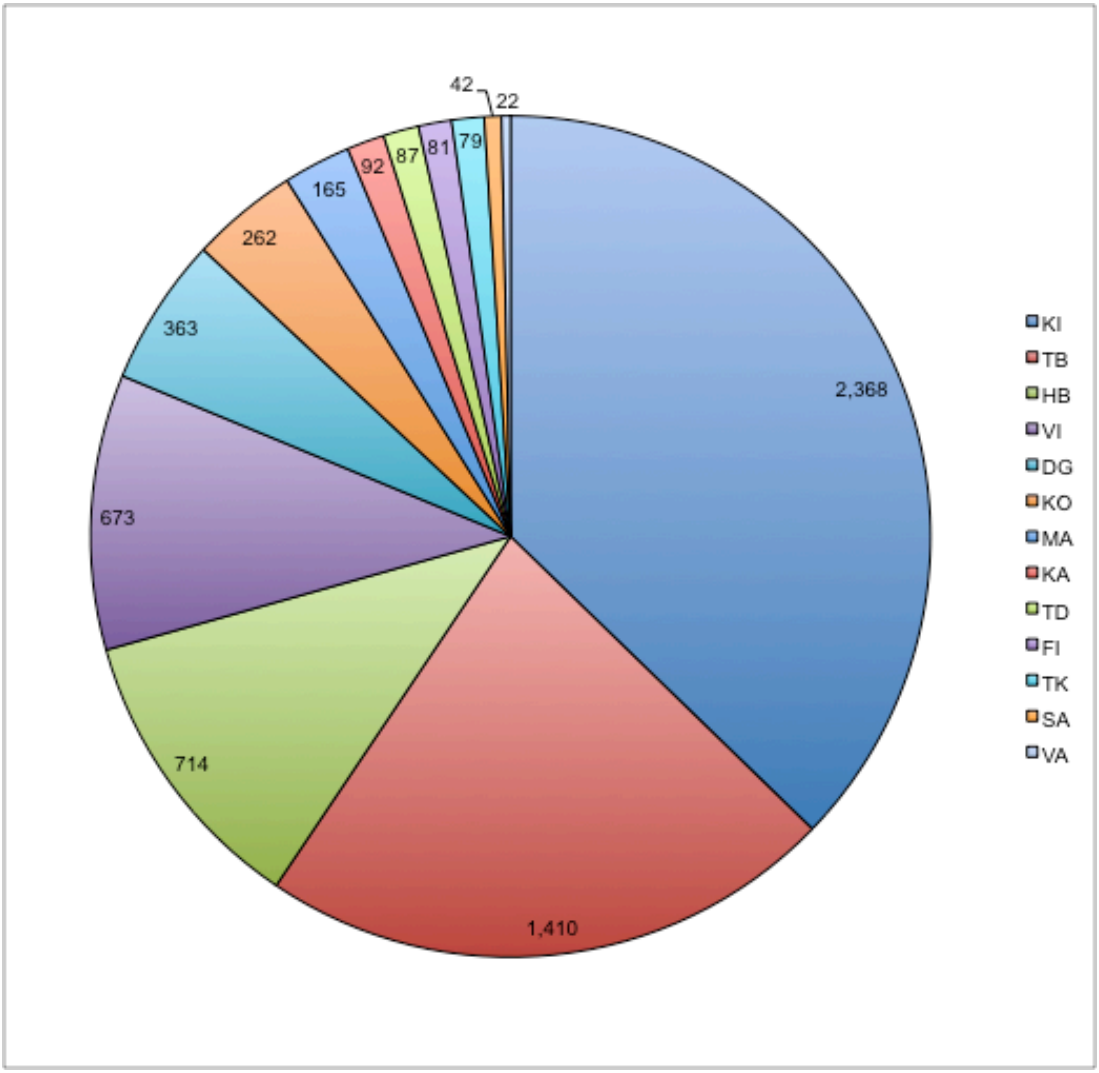


Figure 4.13c Overall species consumption of the four study groups combined.

During the study period, 46 food species were recorded. Table 4.14 presents the top 13 ranked species in terms of feeding time. Dietary diversity among groups will be addressed in the following section. Here, I will examine differences among groups in terms of the reliance on several top species. I chose to examine 13 of the most frequently consumed species (noted by an asterisk in Table 4.5) to focus on foods that represented greater than 1% of the overall diet. The top ten species consumed by each group are also presented here and will be further analyzed in the next sections (Table 4.15).

Table 4.14 Top 13 species eaten. Data includes species from all study groups.

Rank	Malagasy Name/Species	Family	Parts Eaten
1	Kily – *Tamarindus indica*	Cesalpinaceae	FR, LB, YL, FL
2	Vine - *Boerhavia diffusa*		LV
3	Herb - *Metaporana parvifolia*		LV
4	Tratraborondreo – *Grewia leucophylla*	Tiliaceae	FR, LV
5	Kotipoke - *Grewia grevei*	Tiliaceae	FR
6	Mantsaky – *Enterospermum pruinosum*	Rubiaceae	FR
7	Dango – *Tallinella grevei*	Portulacaeae	FR
8	*Azima tetracantha – Azima tetracantha*	Salvadoraceae	FR
9	Katrafay – *Cedrelopsis grevei*	Petaeroxylaceae	FR
10	Tainkafotse – *Grewia franciscana*	Tiliaceae	FR
11	Tsikidrakatse – *Bridelia* sp	Euphorbiaceae	FR
12	Sasavy – *Salvadora augustifolia*	Salvadoraceae	FR
13	Mango (introduced) - *Mangifera indica*	Anacardiaceae	FR

Table 4.15 Top 10 species consumed from each study group.

Group	**Black**		
Rank	**Malagasy Name/Species**	**Family**	**Parts Eaten**
1	Kily – *Tamarindus indica*	Cesalpinaceae	FR, LB, YL, FL
2	Tratraborondreo – *Grewia leucophylla*	Tiliaceae	FR, LV
3	Herb - *Metaporana parvifolia*	Convolvulaceae	LV
4	Dango – *Tallinella grevei*	Portulacaeae	FR
5	Vine - *Boerhavia diffusa*		LV
6	Mantsaky – *Enterospermum pruinosum*	Rubiaceae	FR
7	Kotipoke - *Grewia grevei*	Tiliaceae	FR
8	Tsikidrakatse – *Bridelia* sp.	Euphorbiaceae	FR, LV
9	Katrafay – *Cedrelopsis grevei*	Petaeroxylaceae	FR
10	Mango (introduced) - *Mangifera indica*	Anacardiaceae	FR
Group	**Green**		
Rank	**Malagasy Name/Species**	**Family**	**Parts Eaten**
1	Kily – *Tamarindus indica KI*	Cesalpinaceae	FR, LB, YL, FL
2	Vine *Boerhavia diffusa*	Nyctaginaceae	LV
3	Tratraborondreo – *Grewia leucophylla* TB	Tiliaceae	FR, LV
4	Herb HB	Unknown Herb	LV
5	Kotipoke - *Grewia grevei* KO	Tiliaceae	FR
6	Filofilo – *Azima tetracantha* FI	Salvadoraceae	FR
7	Tainkafotse – *Grewia franciscana*	Malvaceae Juss.	FR
8	Mantsaky – *Enterospermum pruinosum* MA	Rubiaceae	FR
9	Mango (introduced) - *Mangifera indica* MN	Anacardiaceae	FR
10	Katrafay – *Cedrelopsis grevei* KA	Petaeroxylaceae	FR

Group	Light Blue		
Rank	**Malagasy Name/Species**	**Family**	**Parts Eaten**
1	Kily – *Tamarindus indica*	Cesalpinaceae	FR, LB, YL, FL
2	Tratraborondreo – *Grewia leucophylla*	Tiliaceae	FR, LV
3	Vine - *Boerhavia diffusa*	Nyctaginaceae	LV
4	Kotipoke - *Grewia grevei*	Tiliaceae	FR
5	Dango – *Tallinella grevei*	Portulacaeae	FR
6	Tainkafotse – *Grewia franciscana*	Malvaceae Juss.	FR
7	Sasavy – *Salvadora angustifolia*	Salvadoraceae	FR
8	Filofilo – *Azima tetracantha*	Salvadoraceae	FR
9	Mantsaky – *Enterospermum pruinosum*	Rubiaceae	FR
10	Katrafay – *Cedrelopsis grevei*	Petaeroxylaceae	FR
Group	**Teal**		
Rank	**Malagasy Name/Species**	**Family**	**Parts Eaten**
1	Kily – *Tamarindus indica*	Cesalpinaceae	FR, LB, YL, FL
2	Tratraborondreo – *Grewia leucophylla*	Tiliaceae	FR, LV
3	Herb *Metaporana parvifolia*	Convolvulaceae	LV
4	Vine - *Boerhavia diffusa*	Nyctaginaceae	LV
5	Fatra – *Terminalia fatrae*	Combretaceae	FR
6	Katrafay – *Cedrelopsis grevei*	Petaeroxylaceae	FR
7	Mantsaky – *Enterospermum pruinosum*	Rubiaceae	FR
8	Tainkafotse – *Grewia franciscana*	Malvaceae Juss.	FR
9	Kotipoke - *Grewia grevei*	Tiliaceae	FR
10	Sasavy – *Salvadora angustifolia*	Salvadoraceae	FR

Tamarindus indica (vernacular: Kily) has been presented as a fallback species in the literature describing *L. catta* diet for decades (Jolly 1966, Sussman and Rakotozafy 1994,

Sauther 1998, Simmen et al. 2006). During the study period, this species was also of primary importance to each group and proved to have very little variation between groups in terms of time spent feeding on all parts (Figure 4.14). In only one comparison was there a significant difference: only Black Group showed significantly more time spent feeding on *Tamarindus indica* than one other group, Light Blue (Figure 4.14, Table 4.16).

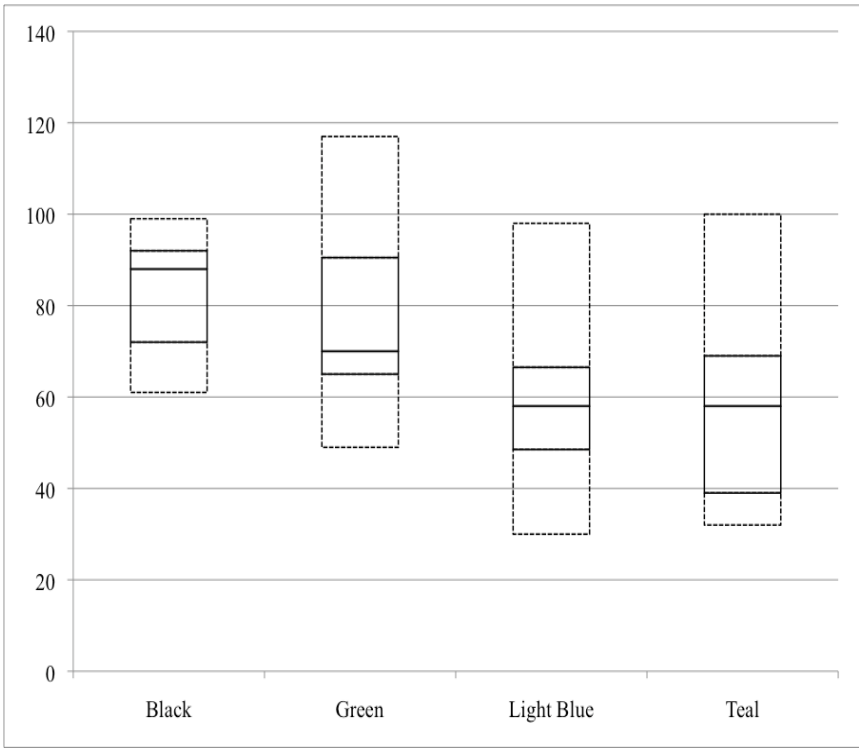


Figure 4.14 Box plots illustrating the median number of feeding instances on *Tamarindus indica*. The Y-axis indicates the number of times individuals were recorded feeding on all parts of *Tamarindus indica*

Table 4.16 Comparison of time spent feeding on all parts of *Tamarindus indica*.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.331	0.5653	N	N
Black vs. Light Blue	6.429	0.0112	N	Y
Black vs. Teal	2.868	0.0903	N	N
Green vs. Light Blue	3.302	0.0692	N	N
Green vs. Teal	2.196	0.1384	N	N
Light Blue vs. Teal	0.020	0.8870	N	N

Not surprisingly from earlier examinations of habitat differences and the effects of grazing and other anthropogenic habitat alterations on food availability, consumption of terrestrial herbs has several important differences among the four study groups (Figure 4.15). Teal Group consumed the highest amount of herbs and significantly more than Light Blue. In fact, all groups consumed significantly more herbs than Light Blue Group (Table 4.17).

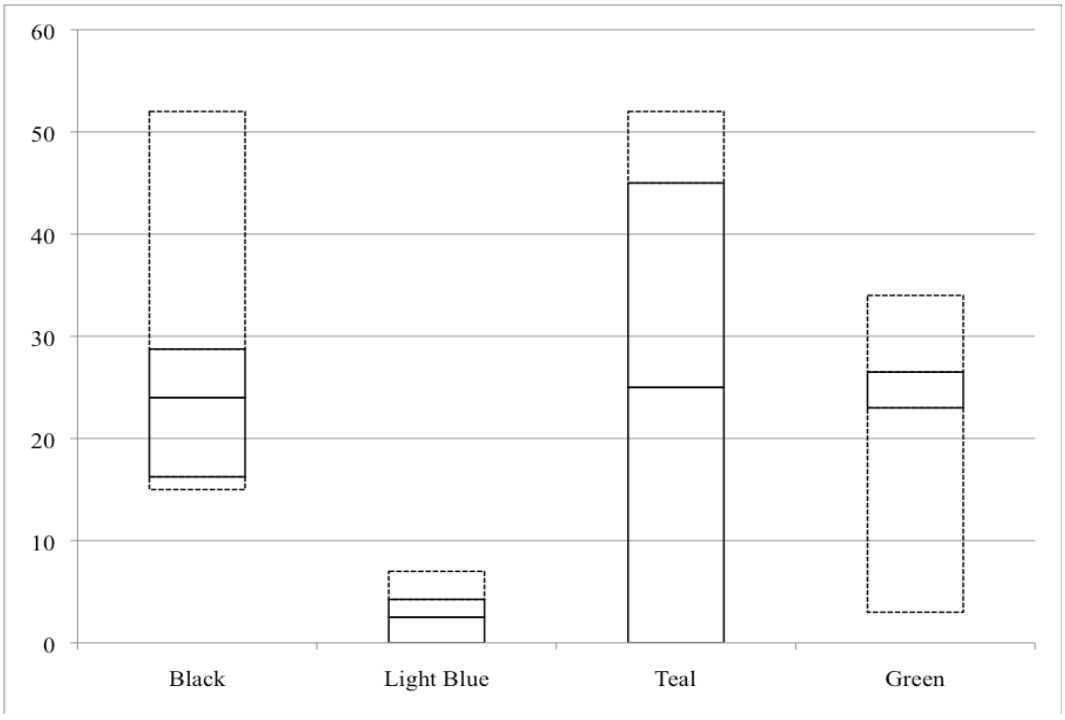


Figure 4.15 Box plots illustrating the medians of the four study groups terrestrial herb consumption. The Y-axis indicates the number of times feeding on terrestrial herbs

Table 4.17 Comparison of time spent feeding on terrestrial herbs.

Group Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.002	0.9611	N	N
Black vs. Light Blue	15.652	0.0001	Y	Y
Black vs. Teal	0.135	0.7133	N	N
Green vs. Light Blue	9.779	0.0018	Y	Y
Green vs. Teal	0.045	0.8323	N	N
Light Blue vs. Teal	2.672	0.1021	N	N

Vines (lianas), were also an important focus of the diet for *L. catta* in the BMSR area. As was apparent in the initial habitat survey and quantitative analysis in Chapter 3, Green Group's habitat had significantly more vines on the sampled trees than other habitats. Consequently, Green Group consumed significantly more of these high-quality leaf resources than other Groups (Figure 4.16, Table 4.18). Figure 4.16 illustrates the similarity of vine consumption among Black, Teal, and Light Blue Groups.

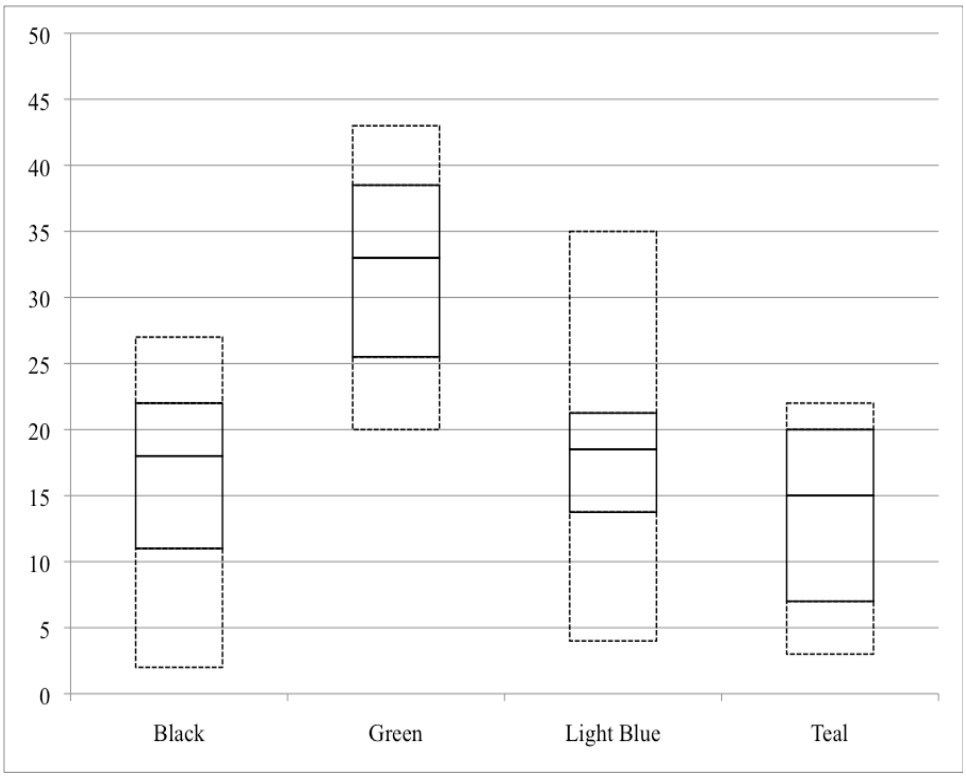


Figure 4.16 Box plots illustrating the medians of the four study groups vine consumption. The Y-axis indicates the number of times feeding on vines.

Table 4.18 Comparisons of time spent feeding on vines.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	6.531	0.0106	N	Y
Black vs. Light Blue	0.114	0.7353	N	N
Black vs. Teal	0.280	0.5966	N	N
Green vs. Light Blue	8.016	0.0046	Y	Y
Green vs. Teal	9.423	0.0021	Y	Y
Light Blue vs. Teal	1.213	0.2707	N	N

Only one group focused on the fruit of *Enterospermum pruinosum* for a significant portion of the diet during the study year: namely, Black Group (Figure 4.17). In fact, when

compared to the consumption of this fruit in other groups, Black Group fed significantly more than any other group (Table 4.19).

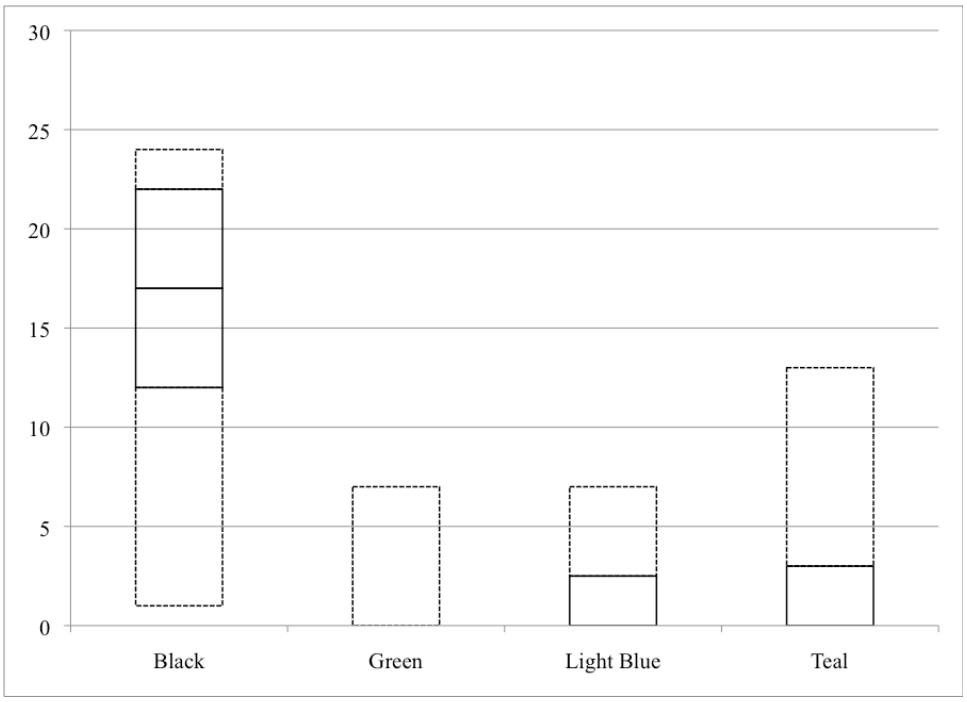


Figure 4.17 Box plots illustrating the medians of the four study groups *Enterospermum pruinosum* fruit consumption. The Y-axis indicates the number of times feeding on this fruit.

Table 4.19 Comparisons of time spent feeding on *Enterospermum pruinosum* fruit.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.016	0.0027	Y	Y
Black vs. Light Blue	10.045	0.0015	Y	Y
Black vs. Teal	7.868	0.0050	Y	Y
Green vs. Light Blue	0.645	0.4220	N	N
Green vs. Teal	0.473	0.4914	N	N
Light Blue vs. Teal	0.000	1.0000	N	N

When available in a group's habitat, *Tallinella grevei* fruit was a significant focus for groups. Green Group lacked this particular understory resource as it appeared to flourish in

slightly drier areas with open canopies. Consequently, Black, Teal, and Light Blue all consumed this fruit more frequently than Green Group (Figure 4.18). Black Group focused on this resource significantly more than each other group (Table 4.20). Teal and Light Blue were similar in their consumption of *Tallinella grevei* fruit (Table 4.20). When these group were pooled with their habitat, Non-Reserve Groups focused significantly more than Reserve Groups on this resource (P<.001).

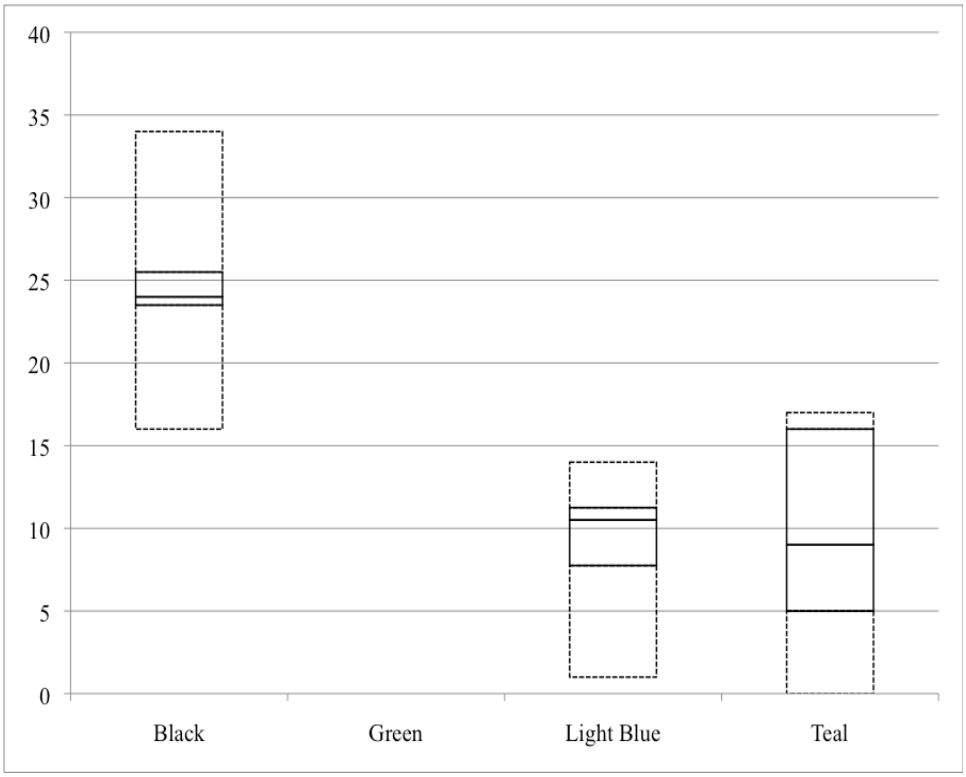


Figure 4.18 Box plots illustrating the medians of the four study groups *Tallinella grevei* fruit consumption. The Y-axis indicates the number of times feeding on this fruit.

Table 4.20 Comparisons of time spent feeding on *Tallinella grevia* fruit.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.800	0.0017	Y	Y
Black vs. Light Blue	12.600	0.0004	Y	Y
Black vs. Teal	9.751	0.0018	Y	Y
Green vs. Light Blue	12.600	0.0004	Y	Y
Green vs. Teal	8.784	0.0030	Y	Y
Light Blue vs. Teal	0.045	0.8312	N	N

Even when compared by study group, Non-Reserve Groups, Black and Light Blue, fed significantly more than both Reserve Groups, Green and Teal on *Grewia grevei* fruit (Figure 4.19 and Table 4.21). This species of tree also grew in more arid, open canopy areas. Not surprisingly, when Reserve and Non-Reserve data were pooled, these differences remained highly significant (P=0.0009).

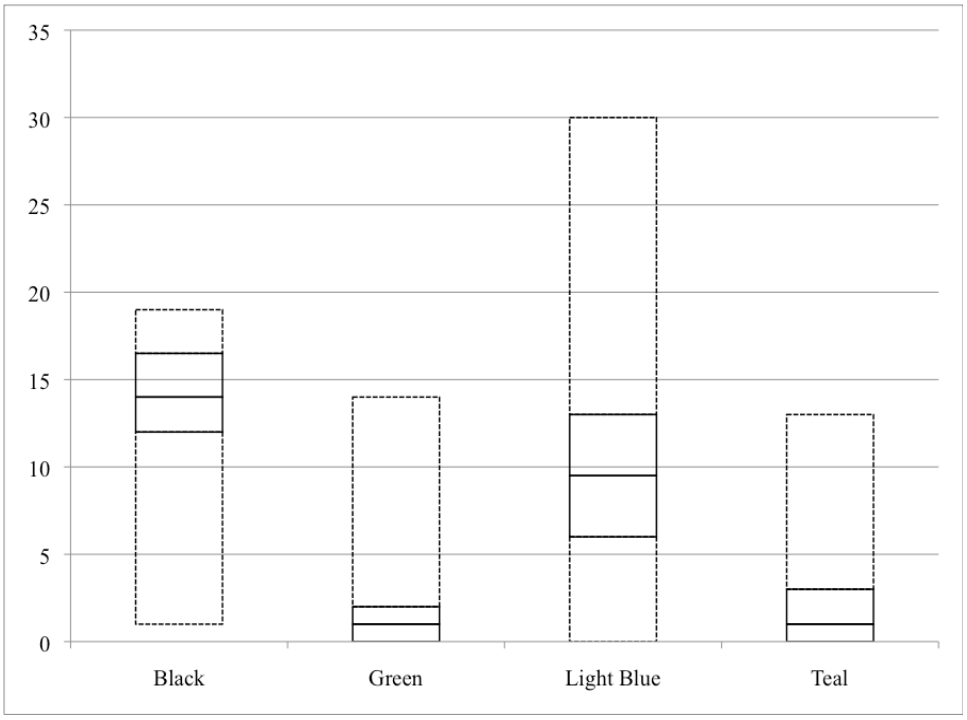


Figure 4.19 Box plots illustrating the medians of the four study groups *Grewia grevei* fruit consumption. The Y-axis indicates the number of times feeding on this fruit.

Table 4.21 Comparisons of time spent feeding on *Grewia grevei* fruit.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	5.894	0.0152	N	Y
Black vs. Light Blue	1.607	0.2049	N	N
Black vs. Teal	7.003	0.0081	Y	Y
Green vs. Light Blue	4.114	0.0425	N	Y
Green vs. Teal	0.137	0.7110	N	N
Light Blue vs. Teal	5.172	0.0230	N	Y

Focus on the *Grewia leucophylla* fruit was fairly even among study groups (Figure 4.20). Even with overlap among the consumption distributions, both Black and Teal Group consumed significantly more of this species than Light Blue (Table 4.22).

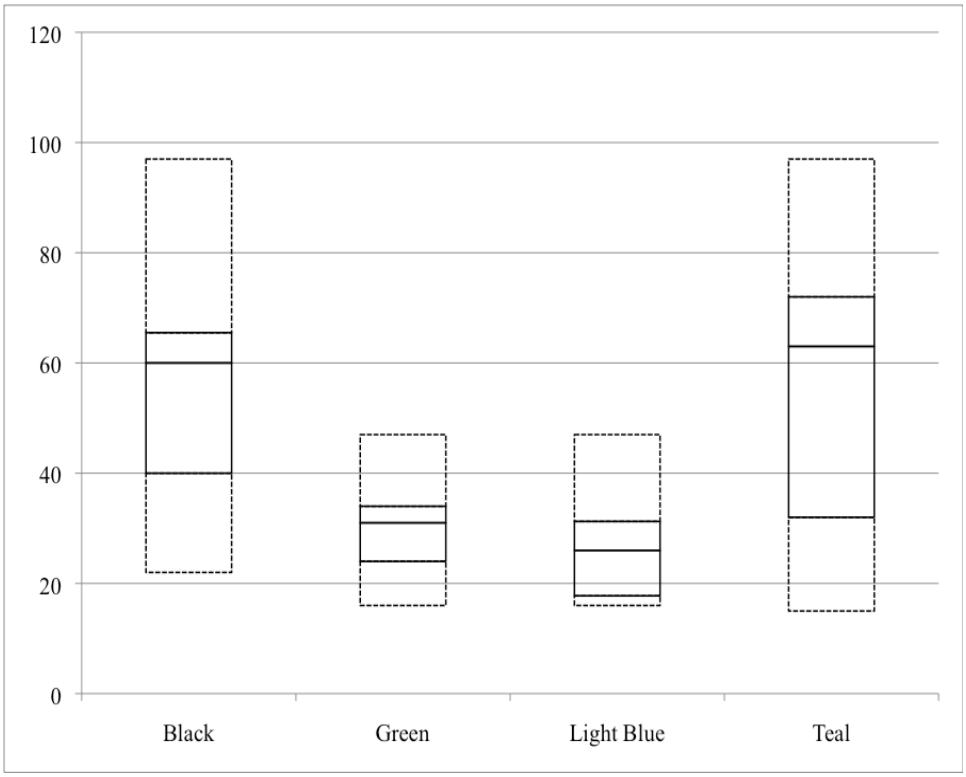


Figure 4.20 Box plots illustrating the medians of the four study groups *Grewia leucophylla* fruit consumption. The Y-axis indicates the number of time feeding on this fruit.

Table 4.22 Comparisons of time spent feeding on *Grewia leucophylla* fruit.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	3.433	0.0639	N	N
Black vs. Light Blue	5.600	0.0180	N	Y
Black vs. Teal	0.011	0.9157	N	N
Green vs. Light Blue	0.645	0.4220	N	N
Green vs. Teal	2.196	0.1384	N	N
Light Blue vs. Teal	4.247	0.0393	N	Y

Species that were apparently quite important for some groups were not even on the menu in other groups. *Bridelia* sp. was one of these species (Figure 4.21). Black Group fed on this species significantly more than each of the other study groups (Table 4.23).

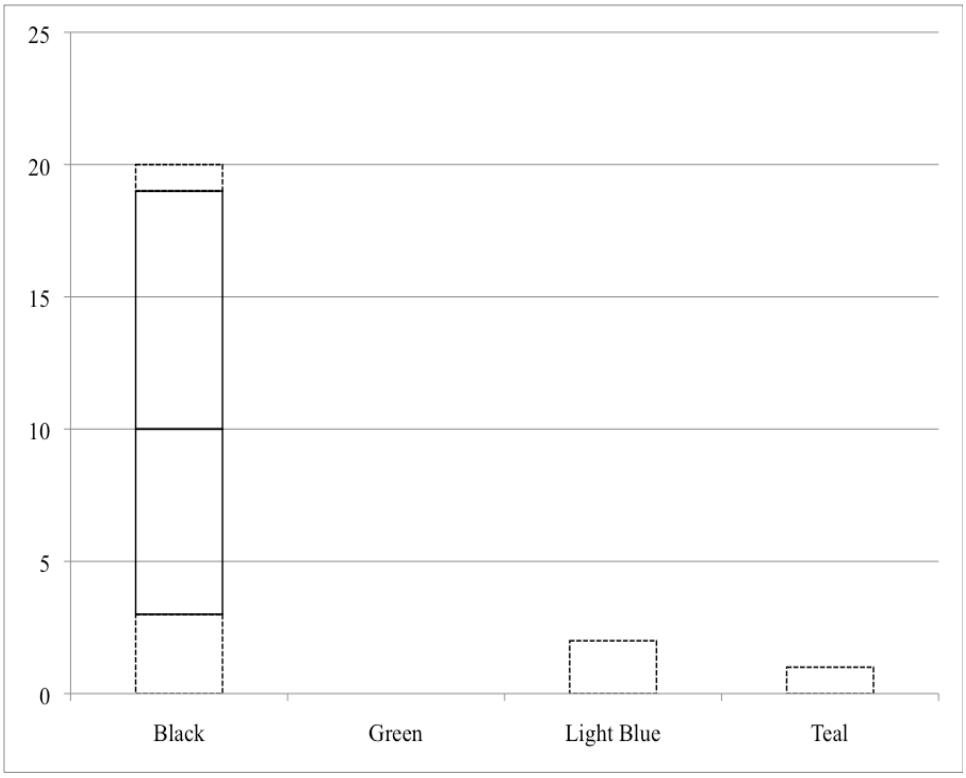


Figure 4.21 Box plots illustrating the medians of the four study groups *Bridelia* sp. fruit consumption. The Y-axis indicates the number of times feeding on this fruit.

Table 4.23 Comparisons of time spent feeding on *Bridelia* sp. fruit.

Comparison	Value of K-W Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	7.200	0.0073	Y	Y
Black vs. Light Blue	8.750	0.0031	Y	Y
Black vs. Teal	7.868	0.0050	Y	Y
Green vs. Light Blue	0.350	0.5541	N	N
Green vs. Teal	0.137	0.7110	N	N
Light Blue vs. Teal	0.081	0.7762	N	N

In the final comparison for differences among consumption of top species, few differences were seen in the *Cedrelopsis grevei* fruit (Figure 4.22). Like the consumption of Kily, only Black Group focused on this species significantly more than did the other groups (Table 4.24).

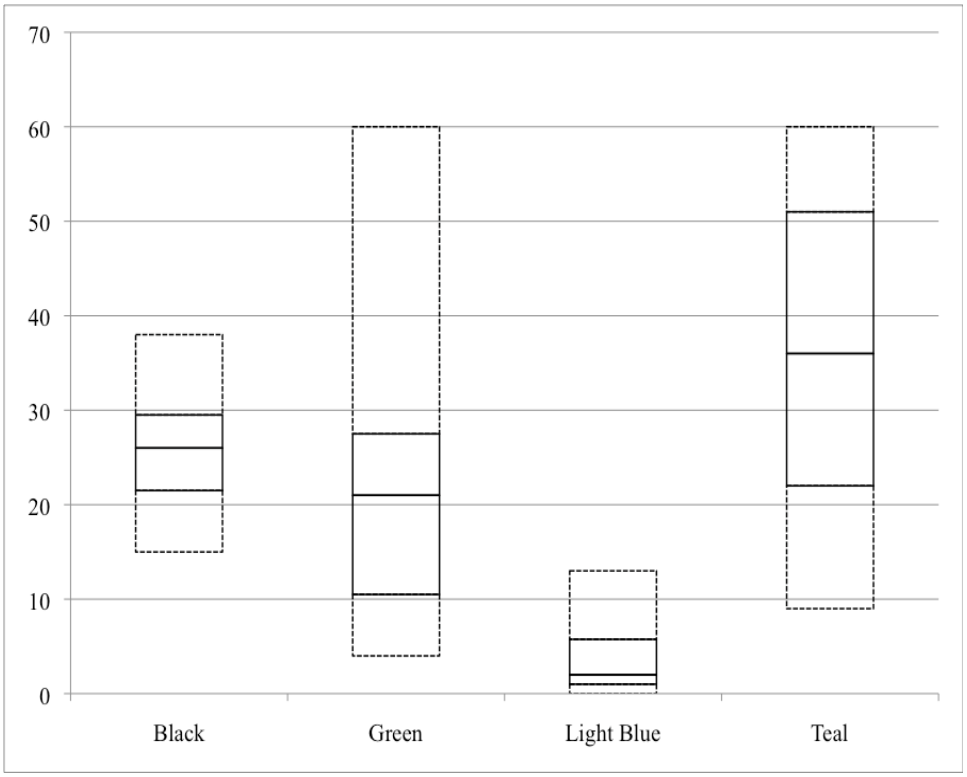


Figure 4.22 Box plots illustrating the medians of the four study groups *Cedrelopsis grevei* fruit consumption. The Y-axis indicates the number of times feeding on this fruit.

Table 4.24 Comparisons of time spent feeding on *Cedrelopsis grevei* fruit.

Comparison	Value of K-W Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	5.894	0.0152	N	Y
Black vs. Light Blue	2.188	0.1391	N	N
Black vs. Teal	1.613	0.2040	N	N
Green vs. Light Blue	2.064	0.1508	N	N
Green vs. Teal	1.751	0.1858	N	N
Light Blue vs. Teal	0.001	0.9717	N	N

4.4.2 Dietary Diversity Among Groups

Similar to the differences between Reserve and Non-Reserve Groups in the comparisons made above, there were also differences in both the number of species consumed by each group and in the diversity of diets (Table 4.25). In terms of the number of individual species utilized at levels greater than one percent of feeding time (thus excluding those species used under that threshold), groups vary a little. For instance, the Non-Reserve Groups consumed a greater number of species, 19 and 16 respectively, than the Reserve Groups. Interestingly, Reserve Groups consumed the same number of species the majority of the time, 13 to be exact. Reserve Groups appear to be relying on a fewer number of species.

In terms of the number of species used, and to what extent, the differences among groups in the BMSR region are perhaps best illustrated by using an index that weights each species by its contribution to the diet (Irwin 2006). Simpson's Index of Diversity was employed for this purpose. When the overall feeding dataset for each group is examined, Black Group has the highest diversity (5.56) followed by Teal (4.67), closely followed by Light Blue (4.39). Green Group's diet contained the lowest diversity (3.53). The lower numbers indicate a greater contribution to the diet of a few important species**.**

Table 4.25 Simpson's Index of Diversity and Species Richness for each of the four group's diets.

Group	Species Diversity: Simpson's Index of Diversity	Species Richness (S) *Number of Species Utilized*
Black	5.56	19
Light Blue	4.39	16
Green	3.53	13
Teal	4.67	13

4.4.3 Taxonomic Composition of Diet: Monthly Diversity

As noted in Chapter 3 and in the preceding discussion, the availability of food resources varies between the seasons. Moreover, as opportunistic omnivores, ring-tailed lemurs are flexible in their diet choices in terms of both plant part and plant species. As a result, taxonomic composition of the diet should vary throughout the year as individuals rely on different species. Results indicate that groups rely heavily on certain species for short amounts of time, and this timely emphasis is not identical among groups. Throughout the study period, most species were a major focus for each group, although not at the same time. While there are differences in the top species focused on for each group (Table 4.15), these differences do not appear significant in the quantitative results. What does appear as significant is the timing of reliance on different species (Figure 4.23 a, b, c, d).

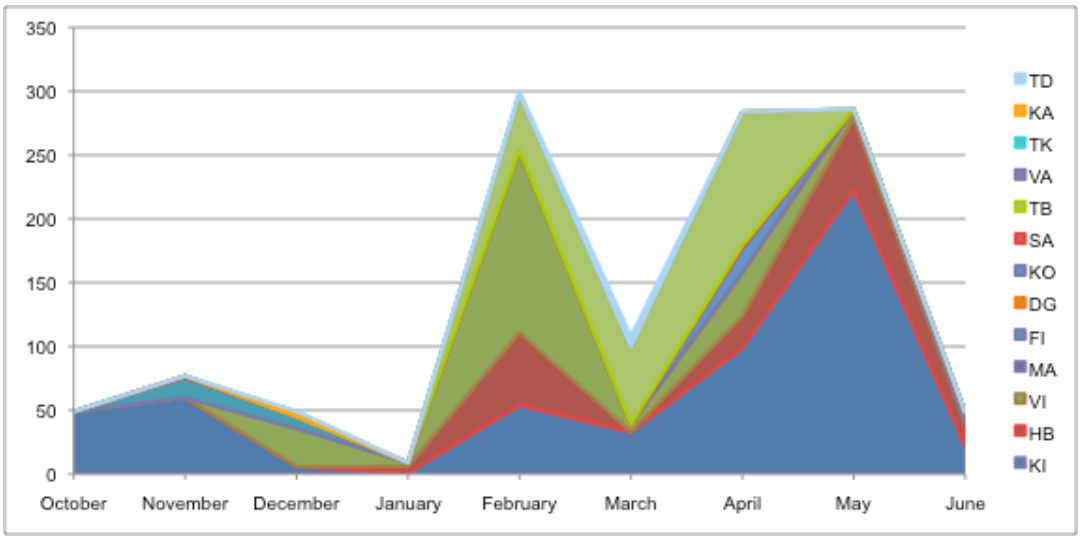


Figure 4.23a Black Group top 13 species in diet for each month.

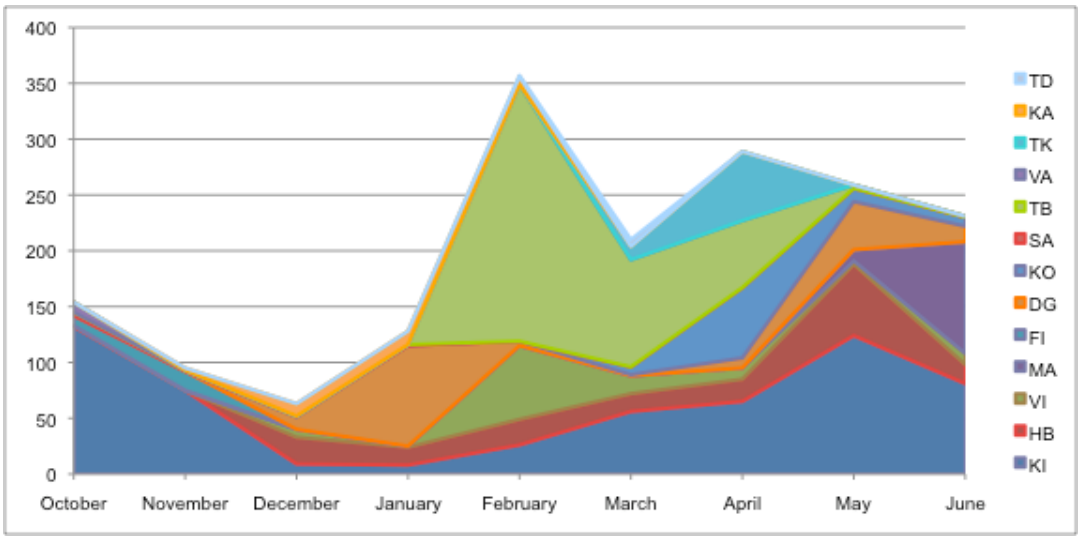


Figure 4.23b Green Group top 13 species in diet each month.

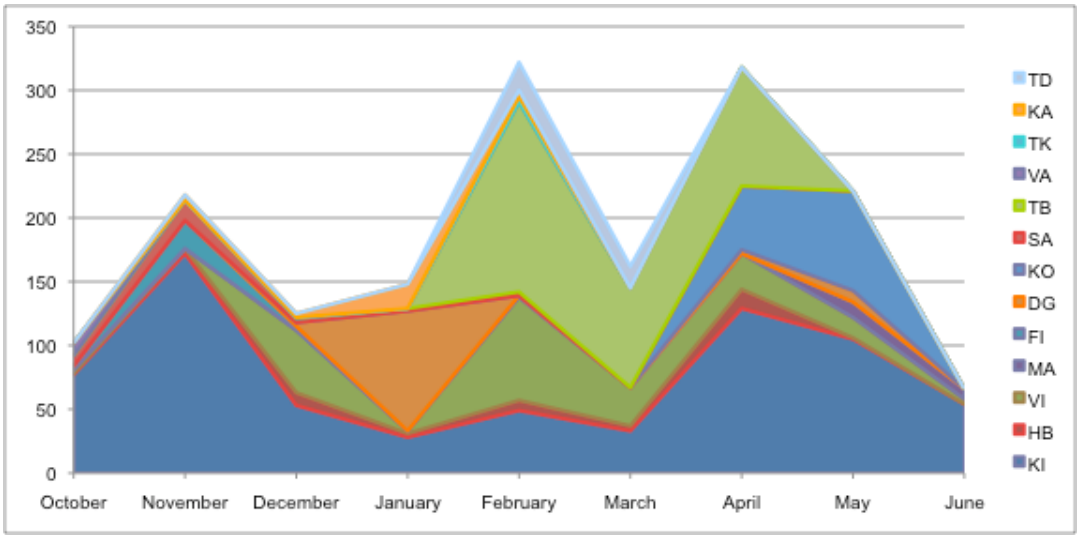


Figure 4.23c Light Blue Group top 13 species in diet each month.

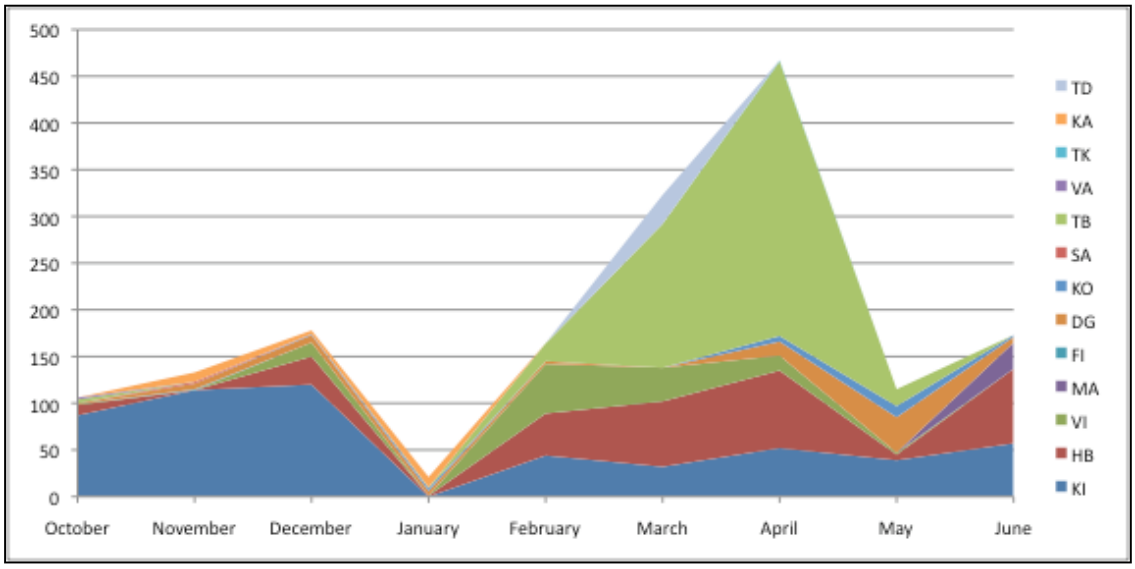


Figure 4.23d Teal Group top 13 species in diet for each month.

As the dry season was drawing to a close, the lemurs in each group relied on Kily (*Tamarindus indica*). Groups near the river, such as Black, Green, and Light Blue, periodically crossed the river to exploit *Azima tetracantha* bushes that were more abundant in areas that were not covered in dense canopy. During December, as the wet season began in earnest, some differences begin to show in how the lemurs are utilizing their habitat. For instance, both Black

and Teal Groups ate more terrestrial herbs than did Green Group (Table 4.26) (Figure 4.24). In addition to terrestrial herbs, Teal Group also relied significantly more on Kily than each of the other groups (Table 4.26) (Figure 4.25).

Table 4.26 Kruskal-Wallis test of terrestrial herb and Tamarind consumption between groups in December.

Herb consumption comparison between groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	5.000	0.0253	N	Y
Black vs. Light Blue	3.002	0.0832	N	N
Black vs. Teal	0.030	0.8622	N	N
Green vs. Light Blue	1.400	0.2367	N	N
Green vs. Teal	4.102	0.0428	N	Y
Light Blue vs. Teal	1.929	0.1649	N	N
Tamarind consumption comparison between groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.261	0.6093	N	N
Black vs. Light Blue	2.188	0.1391	N	N
Black vs. Teal	10.500	0.0012	Y	Y
Green vs. Light Blue	2.716	0.0993	N	N
Green vs. Teal	10.500	0.0012	Y	Y
Light Blue vs. Teal	11.524	0.0007	Y	Y

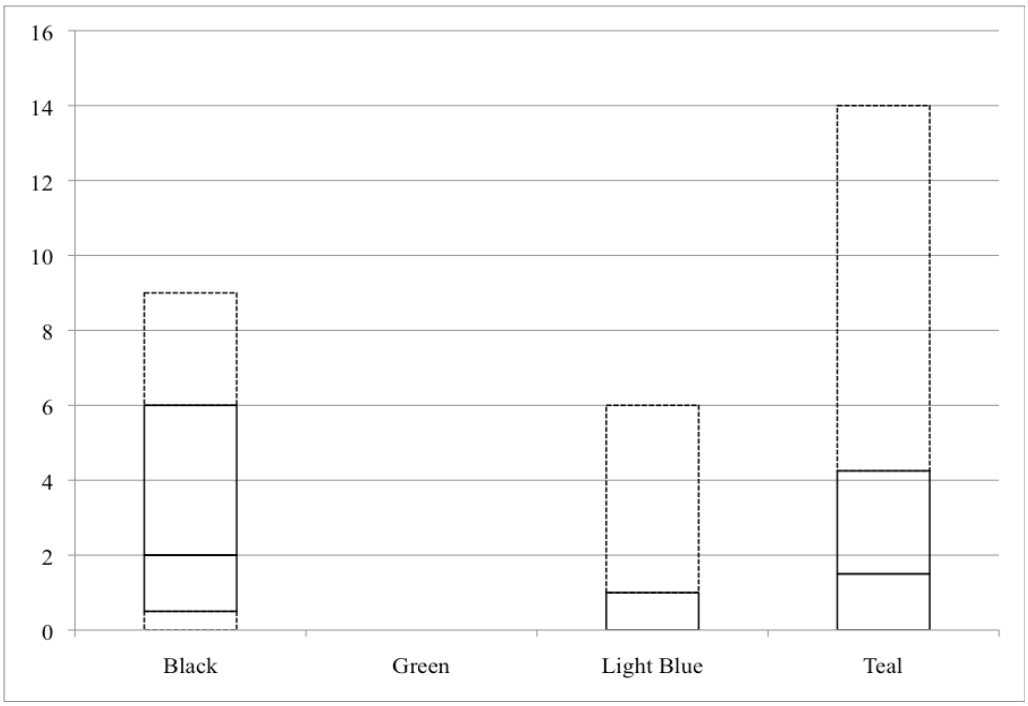


Figure 4.24 Median consumption of herbs by each group in December.

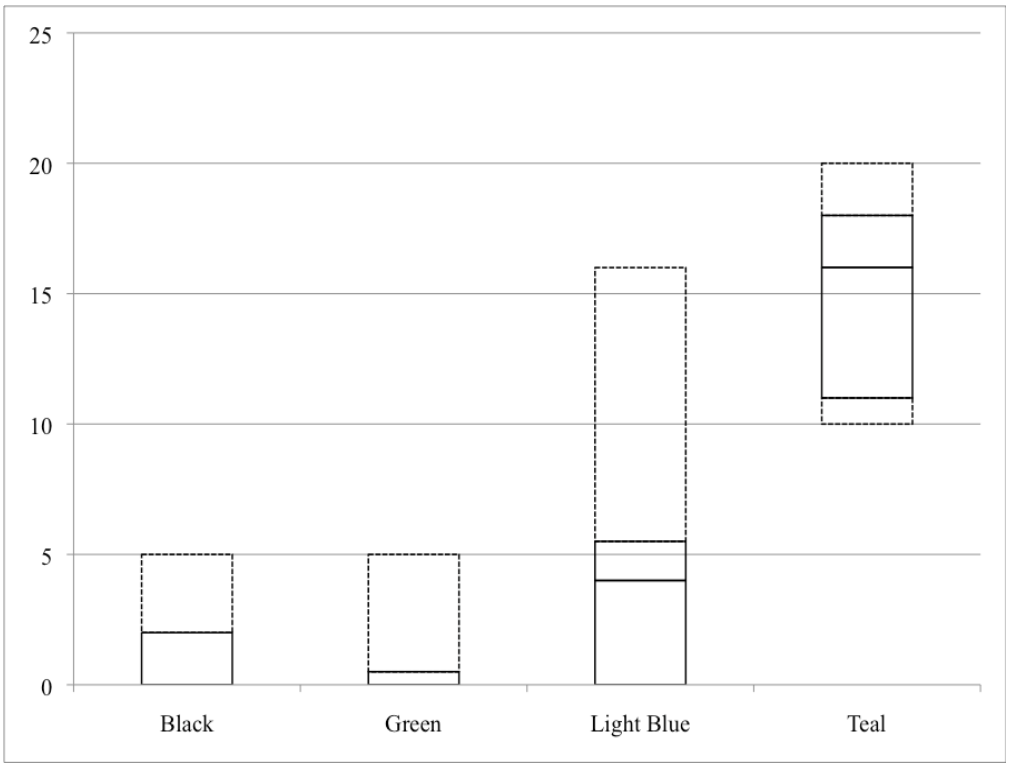


Figure 4.25 Median comparison of *Tamarindus indica* (all-parts) consumption by each group in December.

As the wet season advances into January, both Black and Light Blue Groups focus predominantly on *Tallinella grevia* fruit (Table 4.27, Figure 4.26). This is a 2-4 meter tall tree that tended to grow in drier areas. Notably, *Tallinella grevia* was not as abundant in the home ranges of either Green and Teal. Data from 1987 indicate that Green Group ate significant amounts of this resource. It is likely that the cyclone had a large effect on the phenology of this species. When these data are pooled into Reserve and Non-Reserve Groups, the result remains signficant (K-W test statistic, $P<0.0001$). Unfortunately, data for both Reserve Groups are limited as I was unable to locate them reliably during this month. Anecdotal notes indicate that they varied their diet between several different species during this time, such as vines and herbs, rather than focusing exclusively on a single plant.

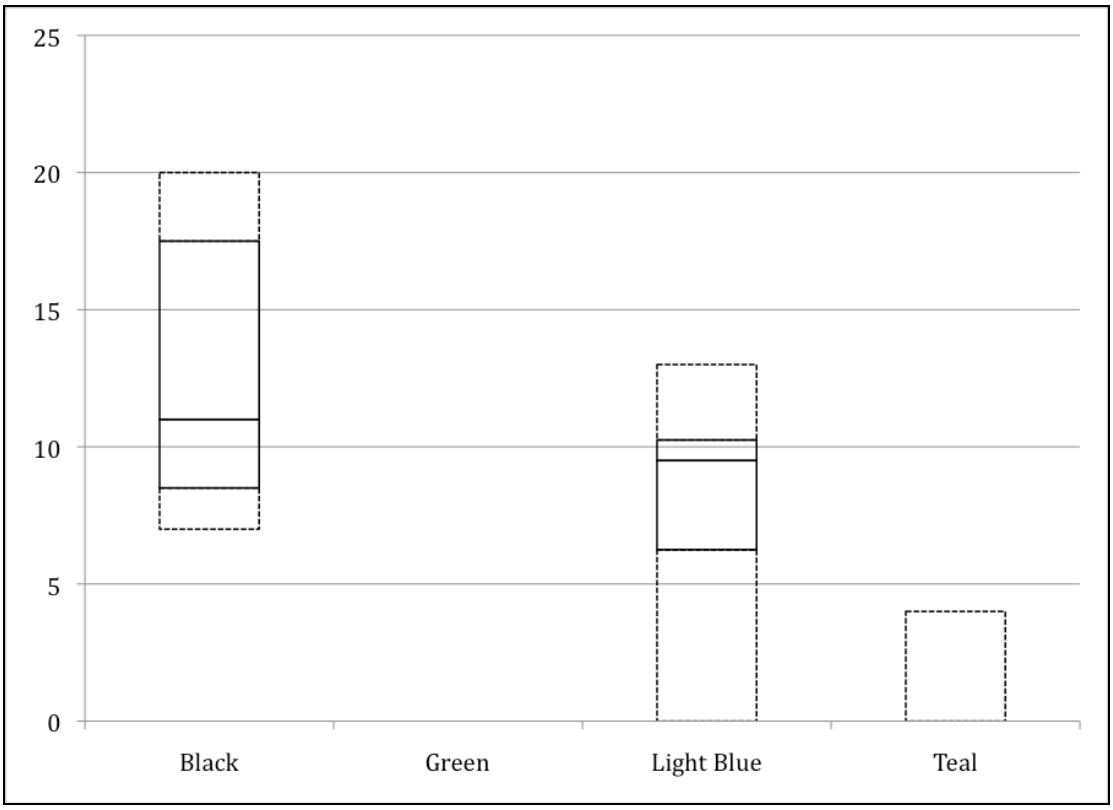


Figure 4.26 Median comparison of *Tallinella grevei* consumption by each group in January.

Table 4.27 Kruskal-Wallis test of *Tallinella grevia* consumption between groups in January.

Comparison of *Tallinella grevei* consumption in January	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	9.800	0.0017	Y	Y
Black vs. Light Blue	2.188	0.1391	N	N
Black vs. Teal	11.118	0.0009	Y	Y
Green vs. Light Blue	10.587	0.0011	Y	Y
Green vs. Teal	0.549	0.4587	N	N
Light Blue vs. Teal	10.920	0.0010	Y	Y

During February, Green and Teal Groups tended to focus more on terrestrial herbs and vines, while Black and Light Blue (not having as many of these resources available) ate fruit from *Grewia leucophylla* and *Grewia franciscana* (Table 4.28) (Figures 4.27, 4.28, 4.29, 4.30). When data are pooled into Reserve vs. Non-Reserve Groups, *Grewia leucophylla* comparisons remain significant (*Grewia leucophylla*, Non-Reserve>Reserve, K-W test statistic 18.247, p = 0.0001). This month's data shows the diversity of species that are available as the primary focus of each group's diet.

Table 4.28 Kruskal-Wallis test of Herb, Vine, *Grewia leucophylla* (fruit), and *Grewia franciscana* consumption between groups in February.

Herb consumption comparison during February	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	1.633	0.2013	N	N
Black vs. Light Blue	1.400	0.2367	N	N
Black vs. Teal	0.473	0.4914	N	N
Green vs. Light Blue	7.545	0.0060	Y	Y
Green vs. Teal	0.630	0.4273	N	N
Light Blue vs. Teal	4.698	0.0302	N	Y
Vine consumption comparison during February	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H0 at 5% sig. level?**
Black vs. Green	6.531	0.0106	N	Y
Black vs. Light Blue	0.714	0.3980	N	N
Black vs. Teal	0.908	0.3408	N	N
Green vs. Light Blue	10.864	0.0010	Y	Y

Green vs. Teal	10.423	0.0012	Y	Y
Light Blue vs. Teal	0.182	0.6698	N	N
Grewia leucophylla **consumption comparison during February**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	9.404	0.0022	Y	Y
Black vs. Light Blue	9.779	0.0018	Y	Y
Black vs. Teal	11.118	0.0009	Y	Y
Green vs. Light Blue	3.945	0.0470	N	Y
Green vs. Teal	3.431	0.0640	N	N
Light Blue vs. Teal	12.626	0.0004	Y	Y
Grewia franciscana **consumption comparison during February**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.004	0.9491	N	N
Black vs. Light Blue	4.464	0.0346	N	Y
Black vs. Teal	0.227	0.6338	N	N
Green vs. Light Blue	3.779	0.0519	N	N
Green vs. Teal	0.227	0.6338	N	N
Light Blue vs. Teal	6.545	0.0105	N	Y

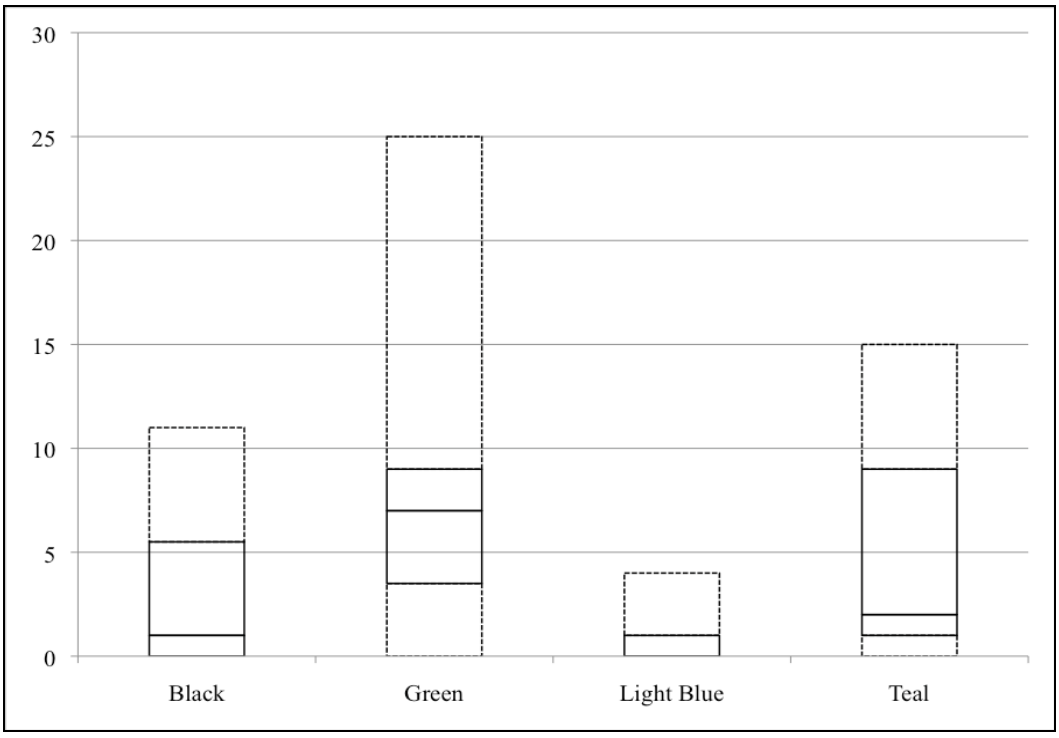


Figure 4.27 Median consumption of herbs by each group in February.

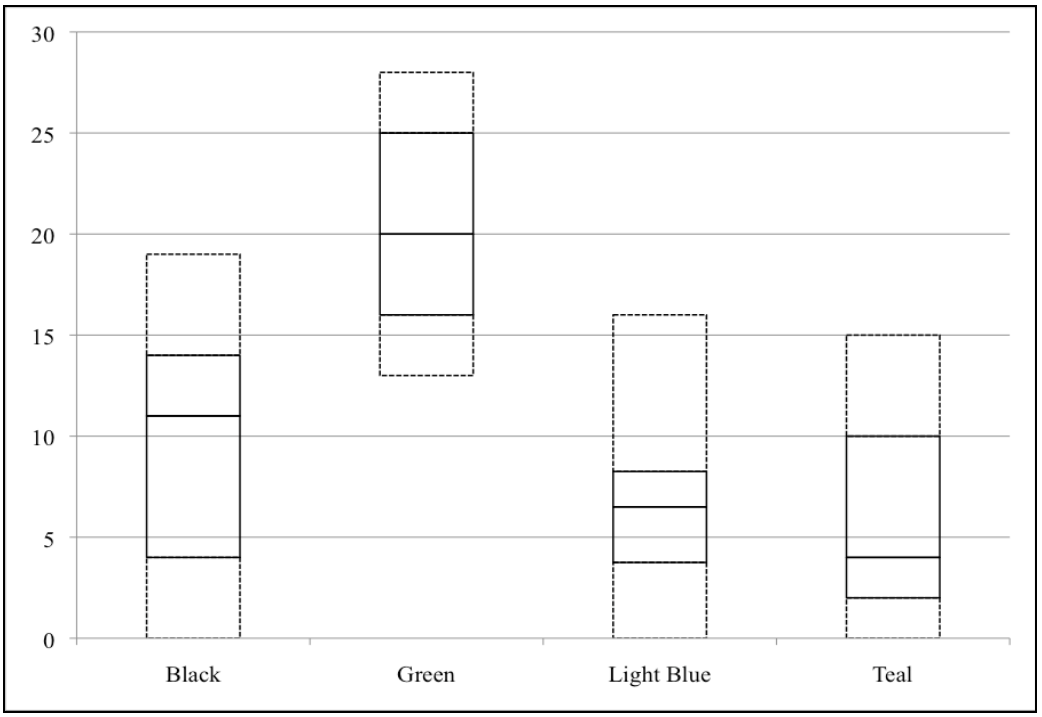


Figure 4.28 Median consumption of vines by each group in February.

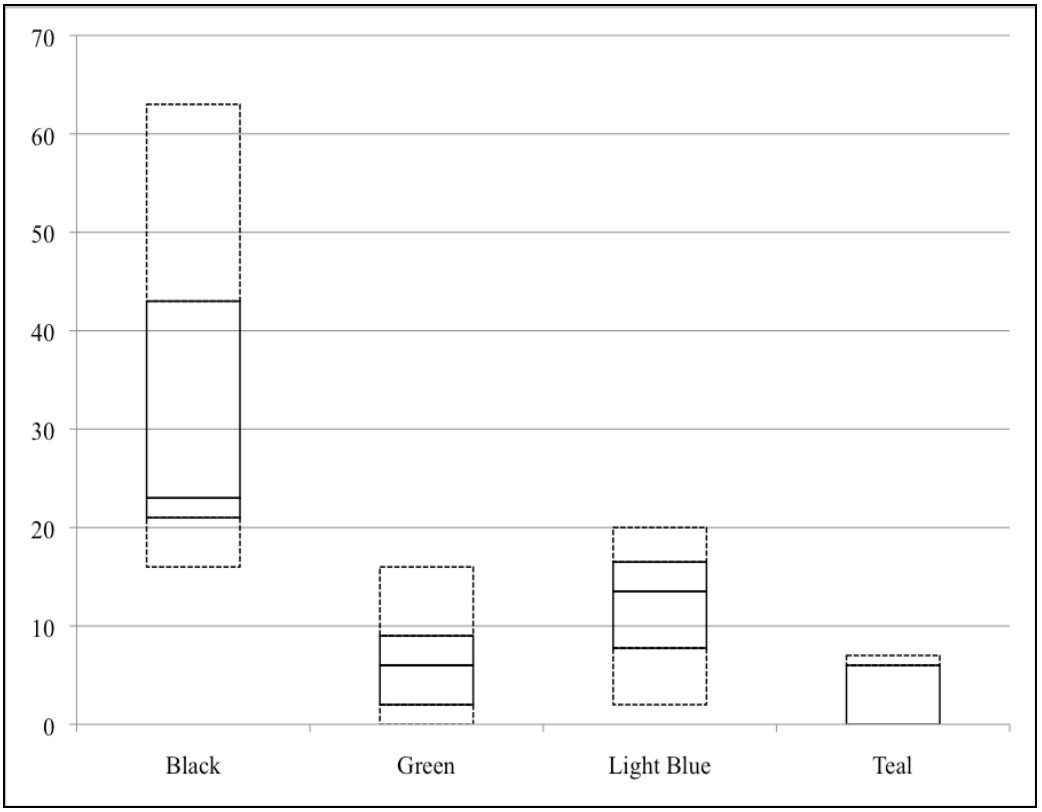


Figure 4.29 Median consumption of *Grewia leucophylla* (fruit) by each group in February.

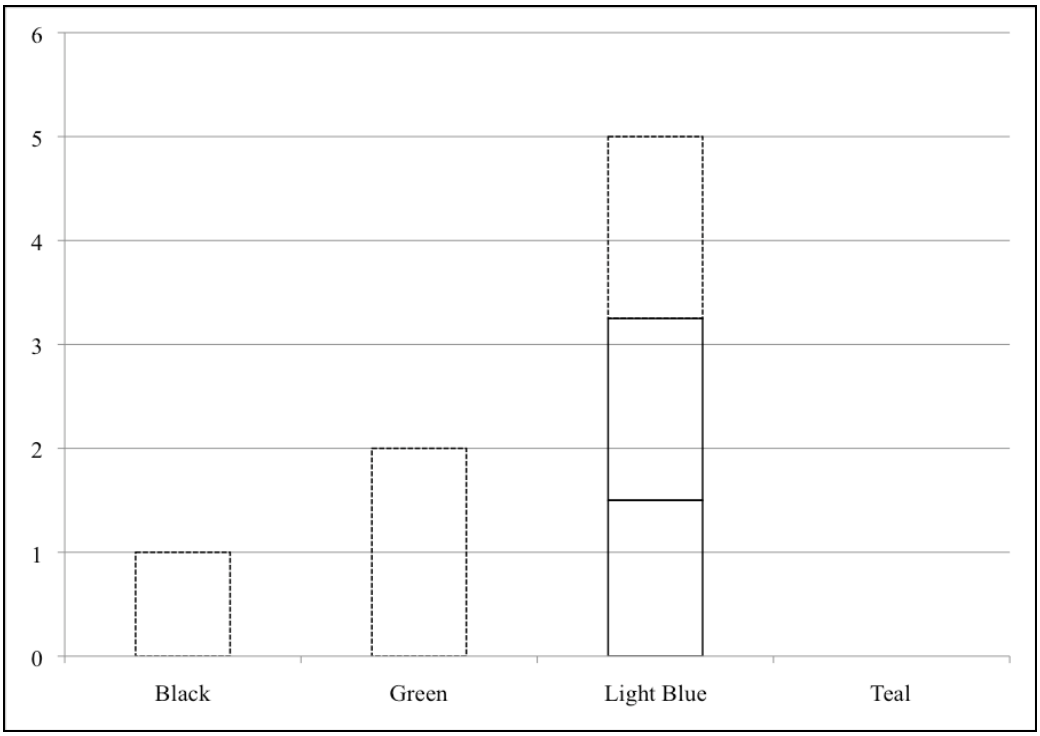


Figure 4.30 Median consumption of *Grewia franciscana* by each group in February.

In the final month of the wet season, groups focused on a wider variety of species. Teal Group, however, was the least diversified during March. Teal relied significantly more on herbs and *Grewia leucophylla* (fruit) than each of the other groups (Table 4.28) (Figure 4.31, 4.32). Green, Black and Light Blue are all focusing on a variety of foods at this time (Figures 4.23a, b, c, d).

Table 4.29 Kruskal-Wallis test of Herb and *Grewia leucophylla* (fruit) consumption between all four groups in March.

Herb consumption comparison between groups in March	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	1.800	0.1797	N	N
Black vs. Light Blue	1.607	0.2049	N	N
Black vs. Teal	3.238	0.0719	N	N
Green vs. Light Blue	0.088	0.7674	N	N
Green vs. Teal	6.725	0.0095	Y	Y
Light Blue vs. Teal	8.284	0.0040	Y	Y
Grewia leucophylla **consumption**	**Value of Test**	**P-Value**	**Reject H_0 at**	**Reject H0 at 5% sig. level?**

comparison between groups in March	Statistic		1% sig. level?	
Black vs. Green	0.690	0.4062	N	N
Black vs. Light Blue	3.150	0.0759	N	N
Black vs. Teal	0.717	0.3971	N	N
Green vs. Light Blue	1.400	0.2367	N	N
Green vs. Teal	5.423	0.0199	N	Y
Light Blue vs. Teal	9.122	0.0025	Y	Y

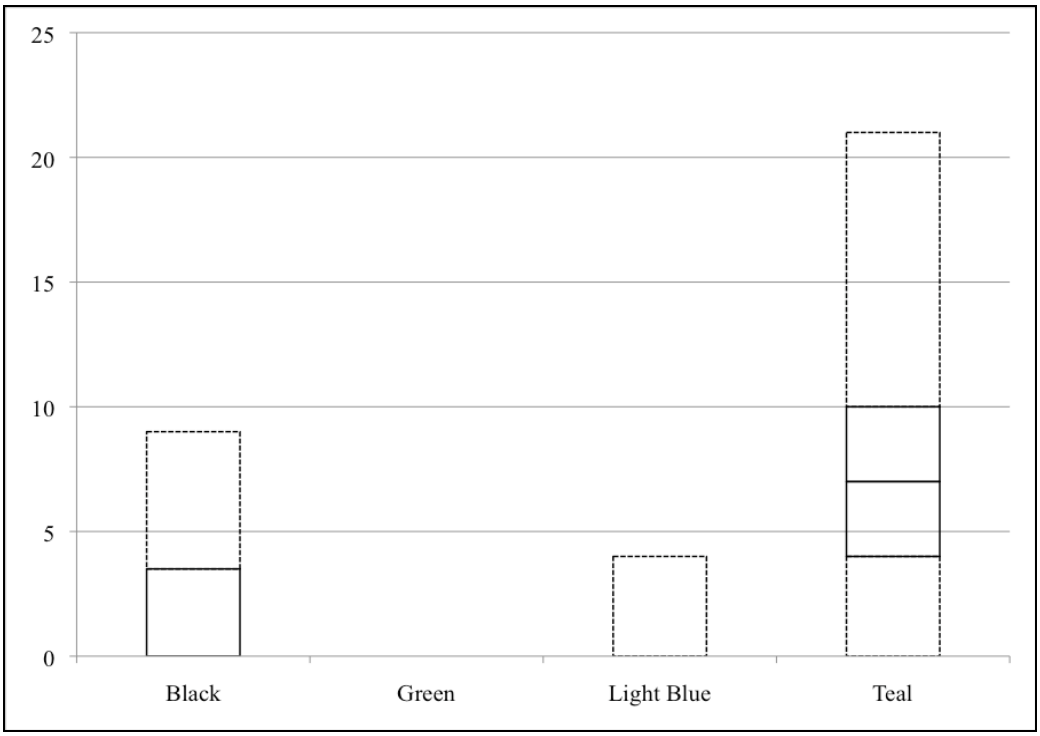


Figure 4.31 Median consumption of Herbs by each group in March.

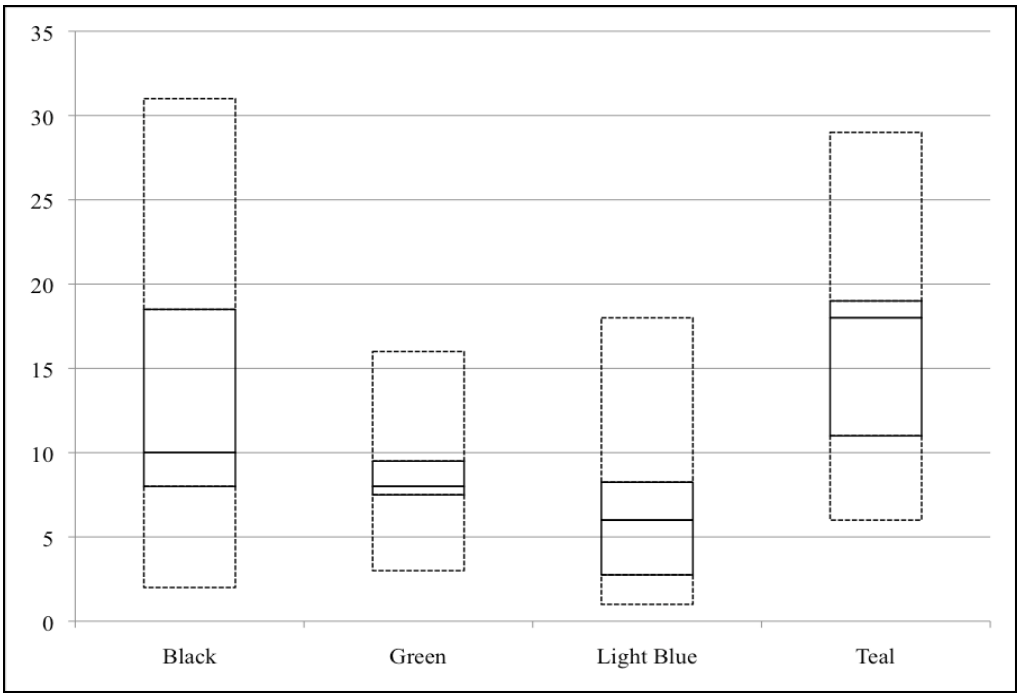


Figure 4.32 Median consumption of *Grewia leucophylla* (fruit) by each group in March.

In April, a few new plants made their appearance in the *L. catta* repertoire of foods. For instance, Black Group fed significantly more on *Grewia grevei* fruit (a small fruit with a large seed and thin pulp) and *Grewia franciscana* than the other groups (Table 4.30) (Figure 4.33, 4.34). Teal Group continued their significant focus on groves of *Grewia leucophylla* fruit in their habitat (Table 4.31) (Figure 4.35).

Table 4.31 Kruskal-Wallis test results for group by group comparisons in April.

***Grewia grevei* consumption comparison between groups in April**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	4.445	0.0350	N	Y
Black vs. Light Blue	4.645	0.0312	N	Y
Black vs. Teal	7.902	0.0049	Y	Y
Green vs. Light Blue	0.257	0.6121	N	N
Green vs. Teal	0.102	0.7494	N	N
Light Blue vs. Teal	0.945	0.3311	N	N
***Grewia leucophylla* consumption**	**Value of Test**	**P-Value**	**Reject H_0 at 1% sig.**	**Reject H_0 at 5% sig.**

comparison between groups in April	**Statistic**		**level?**	**level?**
Black vs. Green	1.800	0.1797	N	N
Black vs. Light Blue	0.002	0.9663	N	N
Black vs. Teal	3.922	0.0476	N	Y
Green vs. Light Blue	2.314	0.1282	N	N
Green vs. Teal	2.551	0.1102	N	N
Light Blue vs. Teal	4.114	0.0425	N	Y
Grewia franciscana **consumption comparison between groups in April**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	7.200	0.0073	Y	Y
Black vs. Light Blue	9.257	0.0023	Y	Y
Black vs. Teal	6.861	0.0088	Y	Y
Green vs. Light Blue	0.000	1.0000	N	N
Green vs. Teal	0.200	0.6547	N	N
Light Blue vs. Teal	0.257	0.6121	N	N

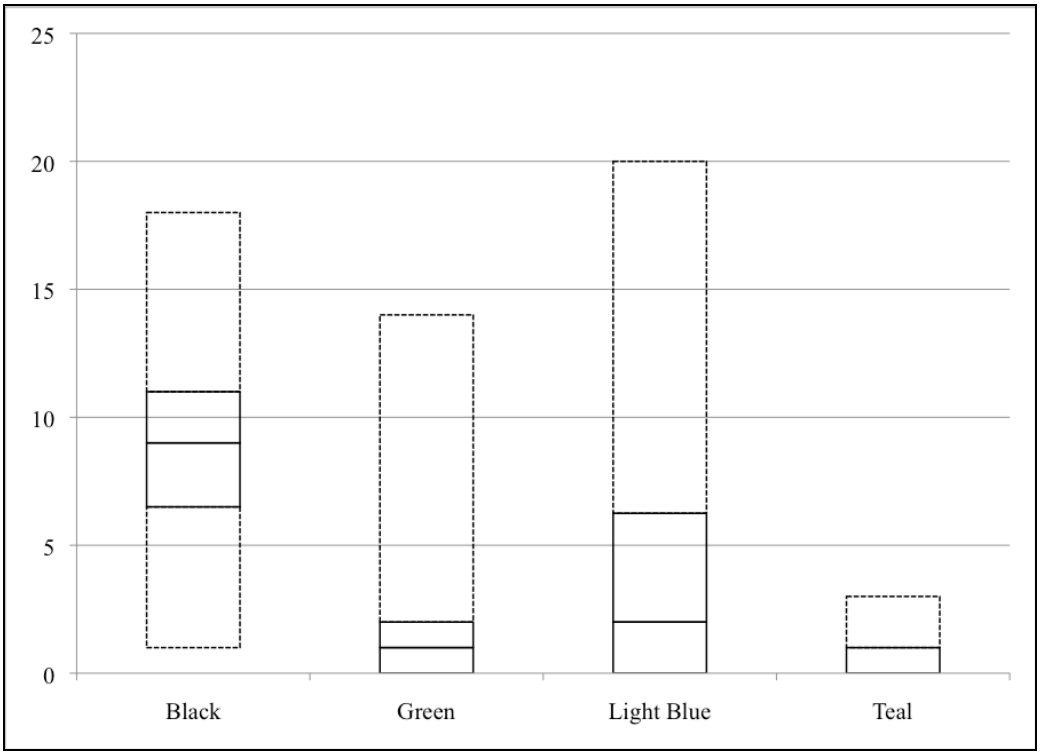


Figure 4.33 Median consumption of *Grewia grevei* fruit by each group in April.

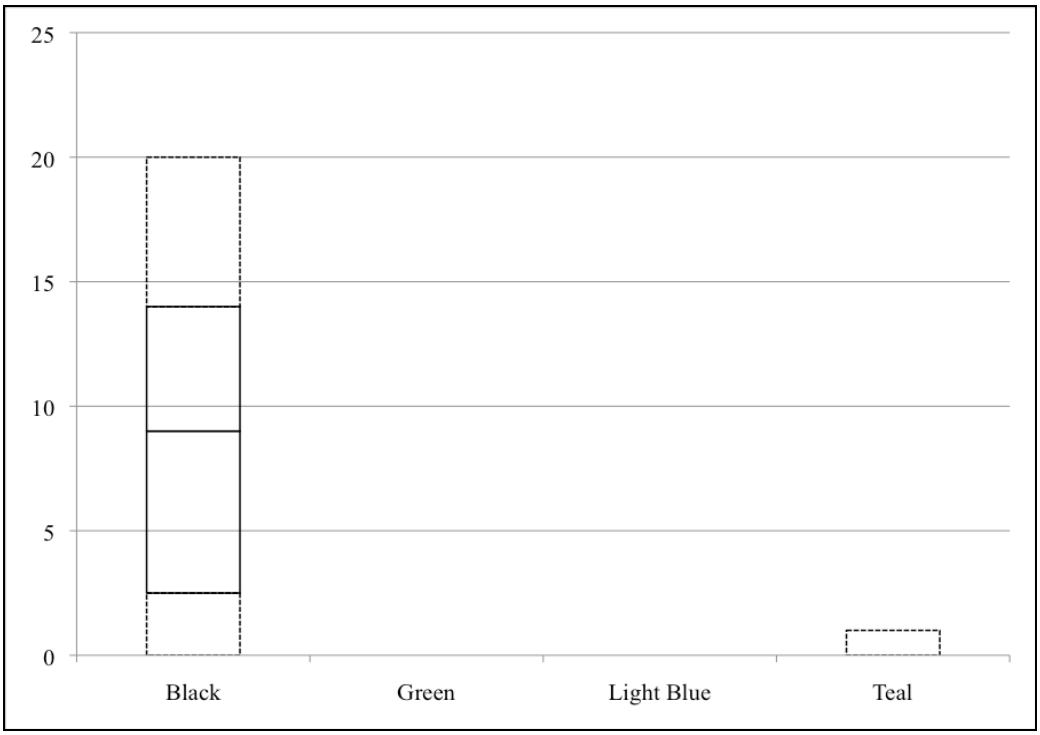


Figure 4.34 Median consumption of *Grewia franciscana* fruit by each group in April.

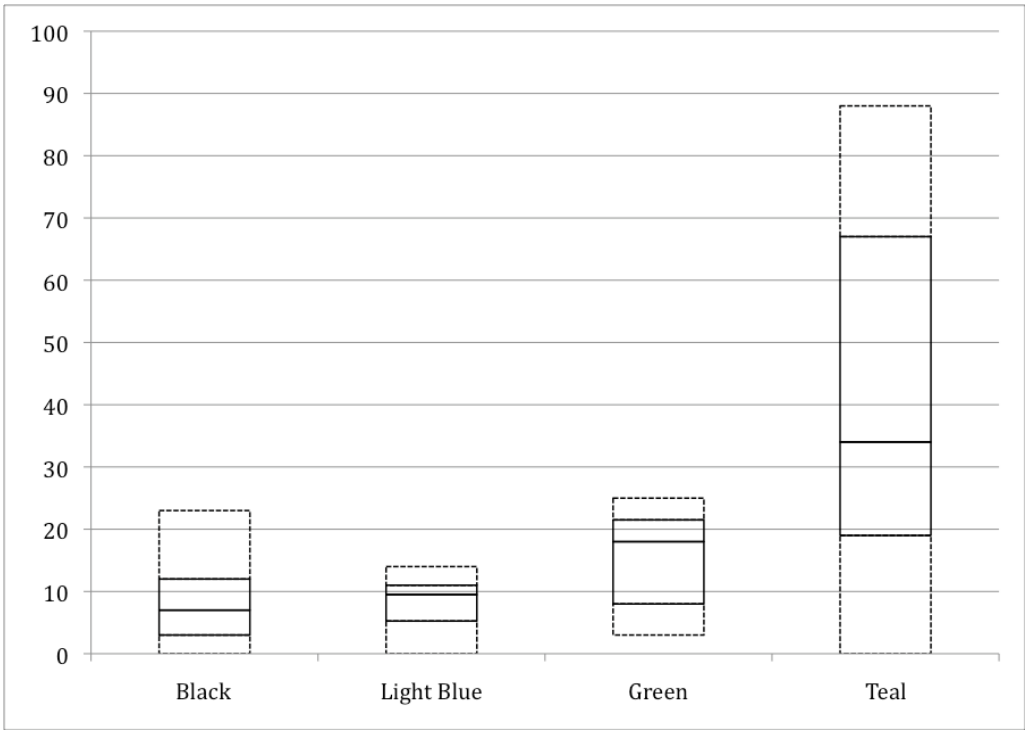


Figure 4.35 Median consumption of *Grewia leucophylla* fruit by each group in April.

As the dry season starts in earnest in May, groups began to focus on resources from *Tamarindus indica* trees (all parts) (Figure 4.36) (Table 4.32). Green Group focused significantly more on all parts of *Tamarindus indica* than the other groups. In addition, both Black and Green relied heavily on leaves from terrestrial herbs (Table 4.32) (Figure 4.37). Black and Teal also consume significantly more *Tallinella grevei* fruit during this time (Figure 4.38) (Table 4.32). These two groups had significant *Tallinella grevei* tree areas in their range. Simultaneously, Light Blue Group consumed significant more *Grewia grevei* fruit, following Black's month of April pattern (Table 4.32, Figure 4.39). This, again, was a species that grew more frequent in drier areas.

Table 4.32 Kruskal-Wallis test results for group by group comparisons in May.

***Tamarindus indica* consumption comparison between groups in May**	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.000	1.0000	N	N
Black vs. Light Blue	9.002	0.0027	Y	Y
Black vs. Teal	5.169	0.0230	N	Y
Green vs. Light Blue	8.750	0.0031	Y	Y
Green vs. Teal	3.798	0.0513	N	N
Light Blue vs. Teal	1.225	0.2684	N	N
Terrestrial herb consumption comparison between groups in May	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	3.200	0.0736	N	N
Black vs. Light Blue	6.864	0.0088	Y	Y
Black vs. Teal	3.488	0.0618	N	N
Green vs. Light Blue	8.502	0.0035	Y	Y
Green vs. Teal	5.169	0.0230	N	Y
Light Blue vs. Teal	0.178	0.6733	N	N
Tallinella grevei **consumption comparison between groups in May**	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	7.200	0.0073	Y	Y
Black vs. Light Blue	7.314	0.0068	Y	Y

Black vs. Teal	0.237	0.6261	N	N
Green vs. Light Blue	0.350	0.5541	N	N
Green vs. Teal	5.169	0.0230	N	Y
Light Blue vs. Teal	5.878	0.0153	N	Y
***Grewia grevei* consumption comparison between groups in May**	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	3.200	0.0736	N	N
Black vs. Light Blue	3.002	0.0832	N	N
Black vs. Teal	0.534	0.4649	N	N
Green vs. Light Blue	7.088	0.0078	Y	Y
Green vs. Teal	0.323	0.5698	N	N
Light Blue vs. Teal	2.336	0.1264	N	N

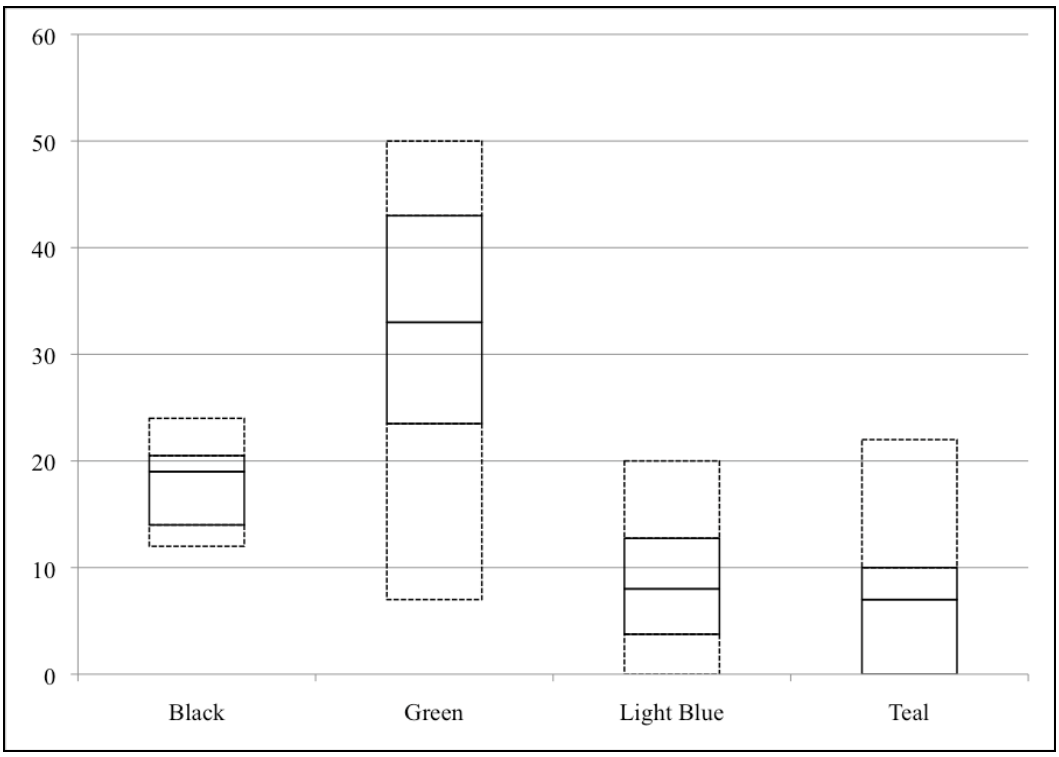


Figure 4.36 Median consumption of *Tamarindus indica* fruit by all groups in May.

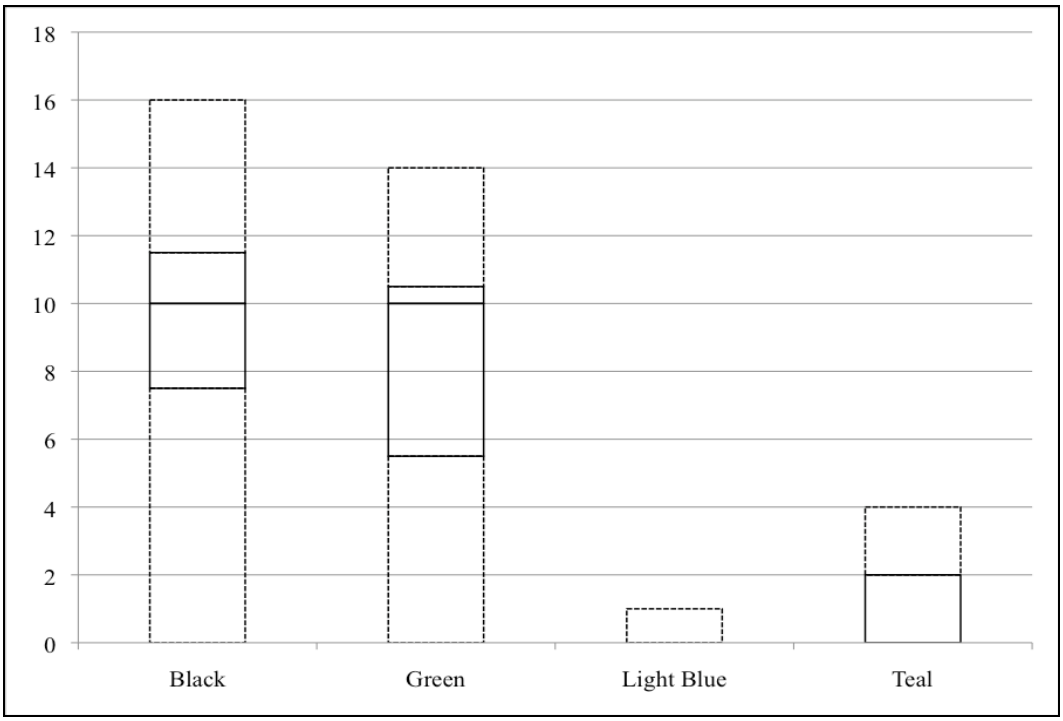


Figure 4.37 Median consumption of terrestrial herbs by all groups in May.

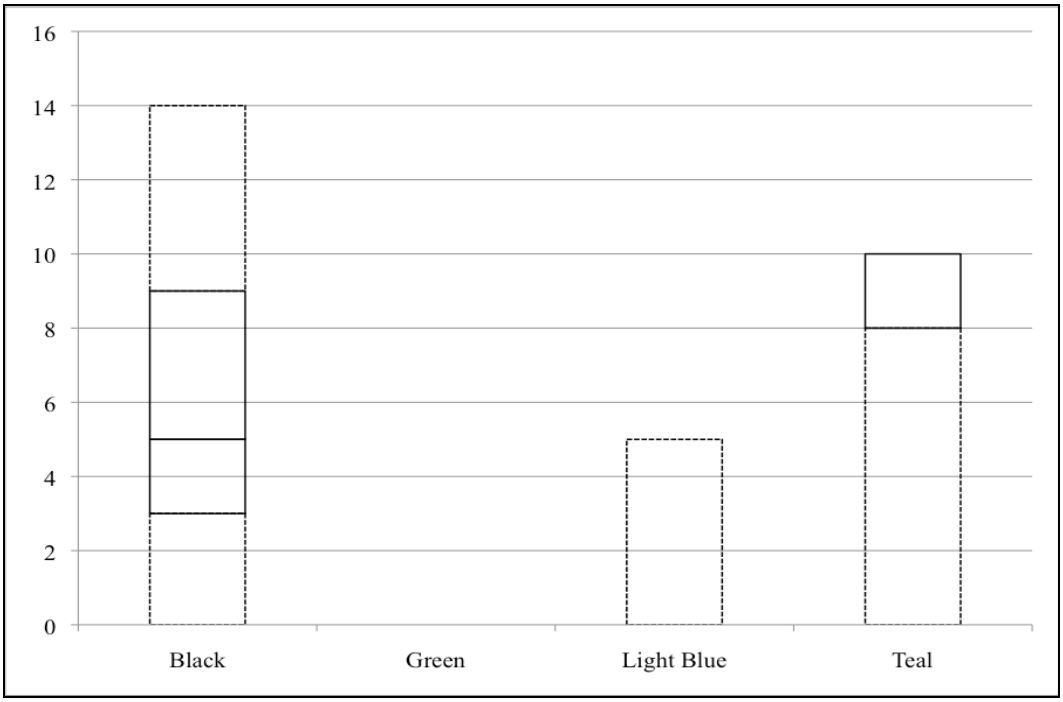


Figure 4.38 Median consumption of *Grewia grevei* fruit by all groups in May.

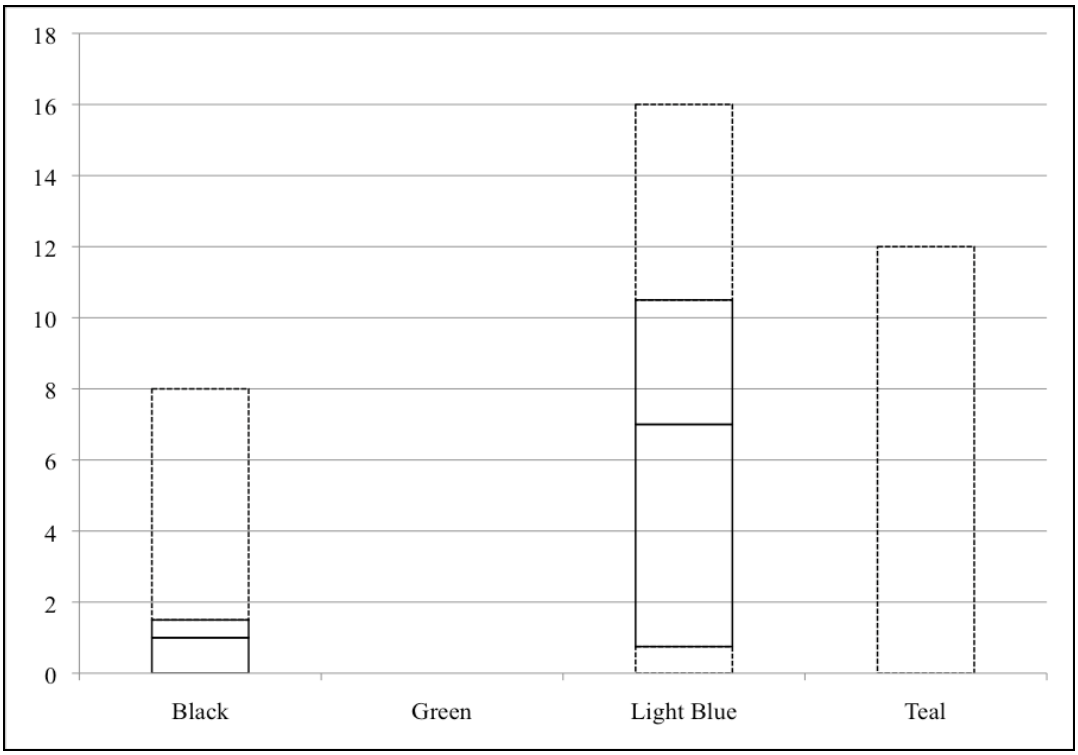


Figure 4.39 Median consumption of *Grewia grevei* fruit by all groups in May.

Finally, in the last month of the study and in one of the driest parts of the year, many individuals began relying on *Tamarindus indica* resources again (Figure 4.40). Black Group, however, was the only group that focused significantly more than any one other group (Table 4.33). Interindividual variability in *Tamarindus indica* consumption is high during this time (Figure 4.40). All groups, except Light Blue, also utilized terrestrial herbs during this time – a pattern that occurred throughout the study period (Figure 4.41, Table 4.33). Whereas all groups consumed some *Enterospermum pruinosum* fruit during June, Black Group relied heavily on this resource (Table 4.33, Figure 4.42).

Table 4.33 Kruskall-Wallis test results for group to group comparisons in June.

Tamarindus indica **consumption comparison between groups in June**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	4.718	0.0298	N	Y
Black vs. Light Blue	7.088	0.0078	Y	Y
Black vs. Teal	0.735	0.3914	N	N
Green vs. Light Blue	1.400	0.2367	N	N
Green vs. Teal	5.224	0.0223	N	Y
Light Blue vs. Teal	3.167	0.0752	N	N
Herb consumption comparison between groups in June	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.200	0.6547	N	N
Black vs. Light Blue	4.114	0.0425	N	Y
Black vs. Teal	4.903	0.0268	N	Y
Green vs. Light Blue	1.029	0.3105	N	N
Green vs. Teal	4.903	0.0268	N	Y
Light Blue vs. Teal	7.895	0.0050	Y	Y
Enterospermum pruinosum **consumption comparison between groups in June**	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	9.016	0.0027	Y	Y
Black vs. Light Blue	10.864	0.0010	Y	Y
Black vs. Teal	5.224	0.0223	N	Y
Green vs. Light Blue	0.064	0.7998	N	N
Green vs. Teal	1.306	0.2531	N	N
Light Blue vs. Teal	1.371	0.2417	N	N

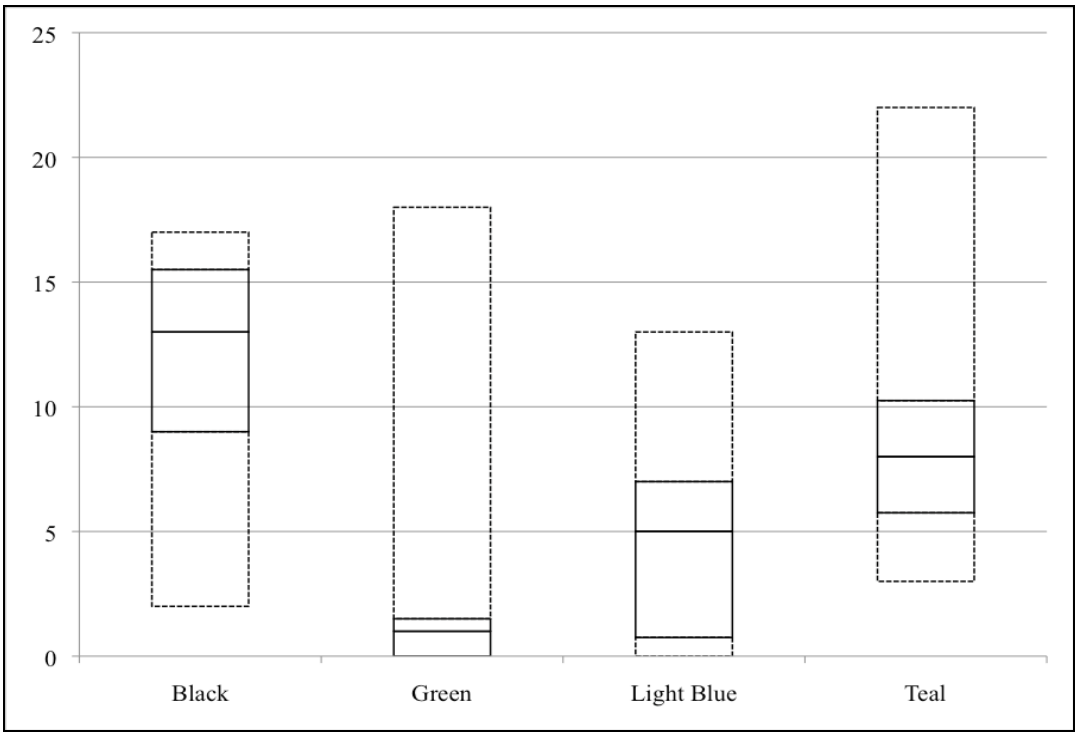


Figure 4.40 Median consumption of *Tamarindus indica* (tamarind) fruit by all groups in June.

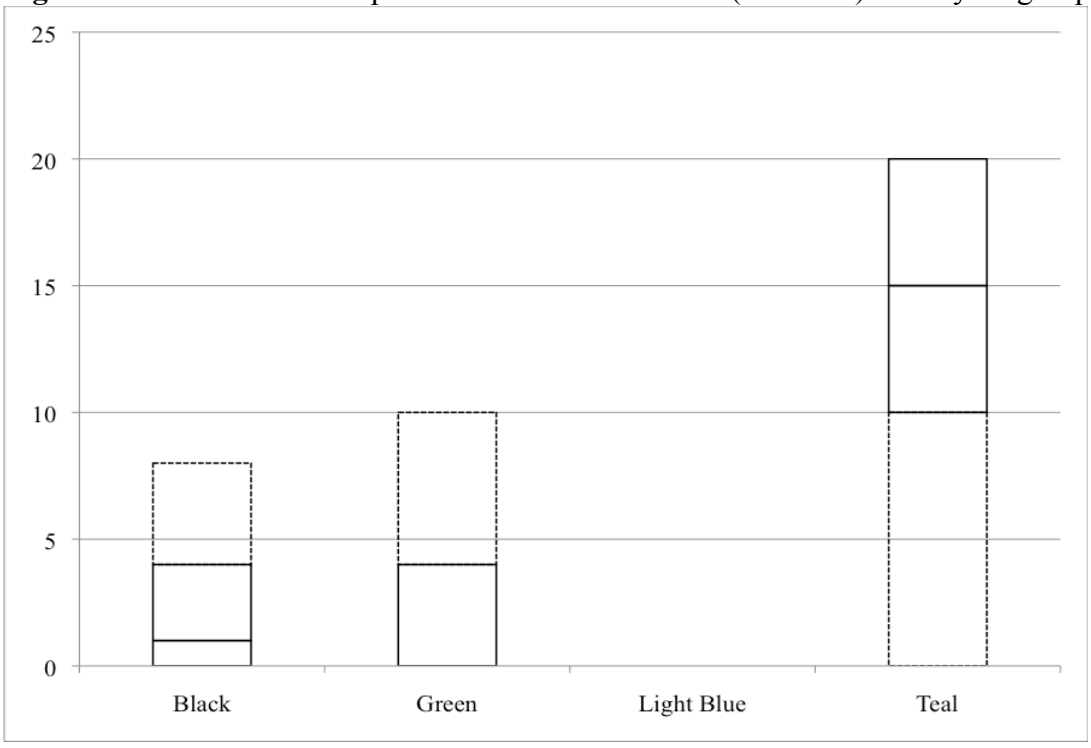


Figure 4.41 Median consumption of Terrestrial Herbs by all groups in June.

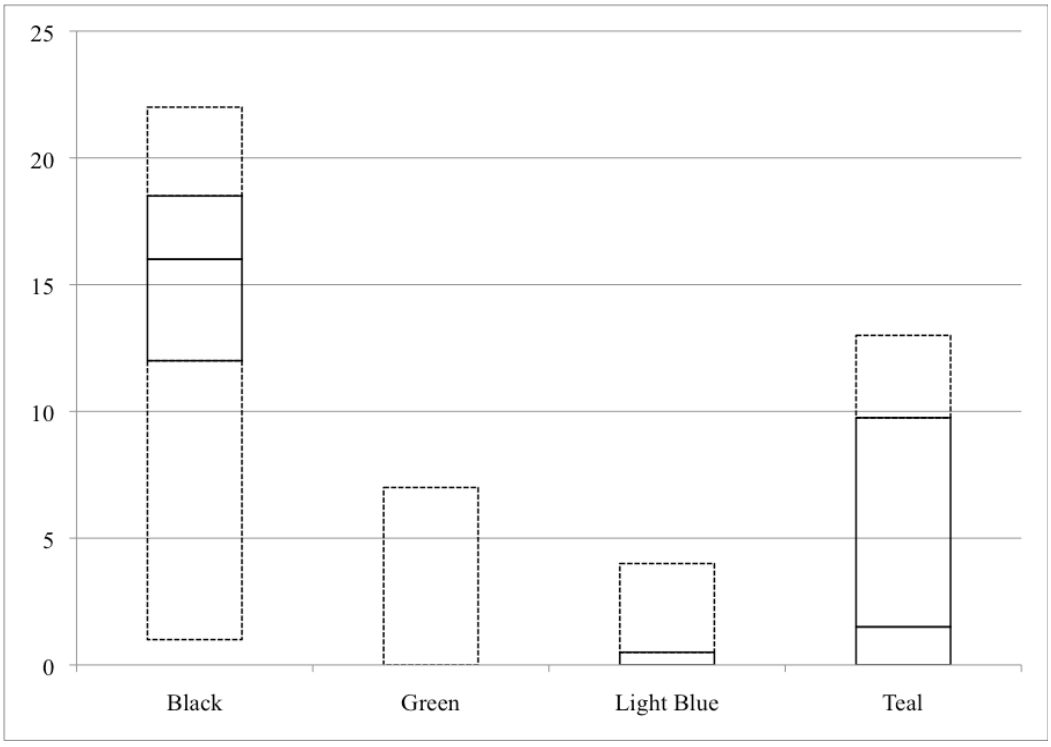


Figure 4.42 Median consumption of *Enterospermum pruinosum* fruit by all groups in June.

4.5 Feeding Strategy: Time spent feeding and foraging

4.5.1 Differences Among Groups

Because food species differ in many variables (e.g. spatial distribution, patch size, relative food availability and food quality), any differences, or lack thereof, in species composition of diets and plant part consumption, may lead to differences in foraging strategy. In daily follows, I recorded incidents of feeding and foraging during my focal individual follows. Table 4.34 and 4.35, and Figures 4.43 and 4.44 show the results of statistical tests for differences among groups in both feeding and foraging incidents.

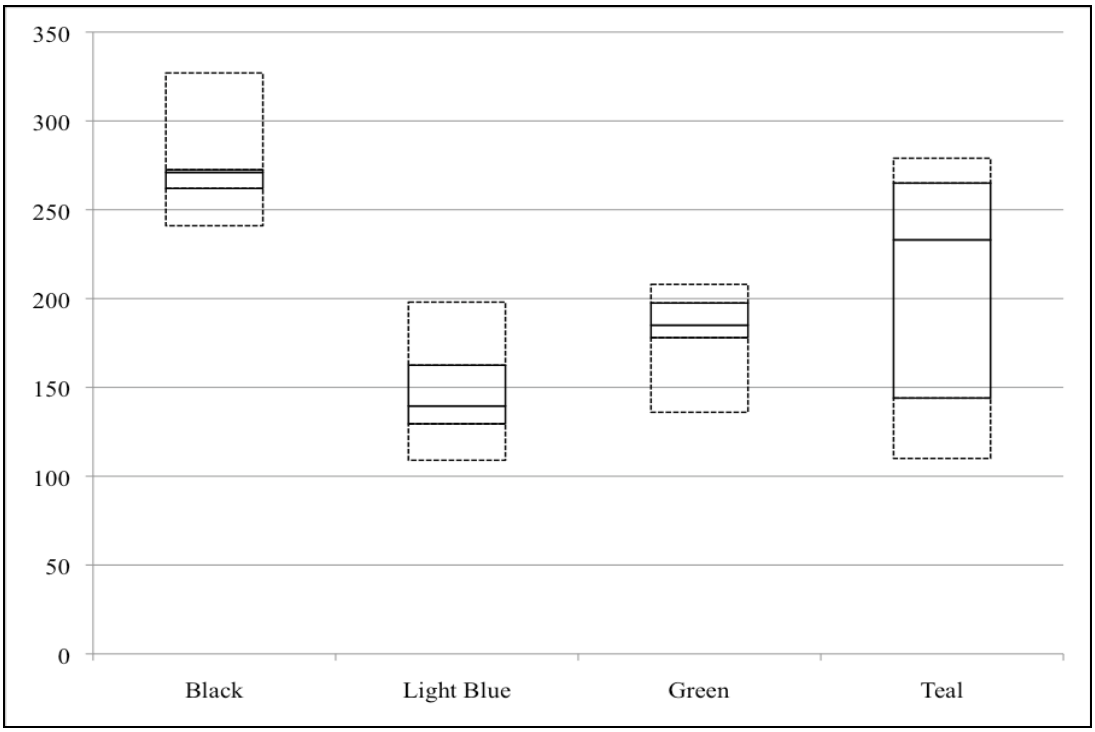


Figure 4.43 Box plot showing medians of observed instances of feeding. Y-axis indicates the number of times individuals were observed feeding.

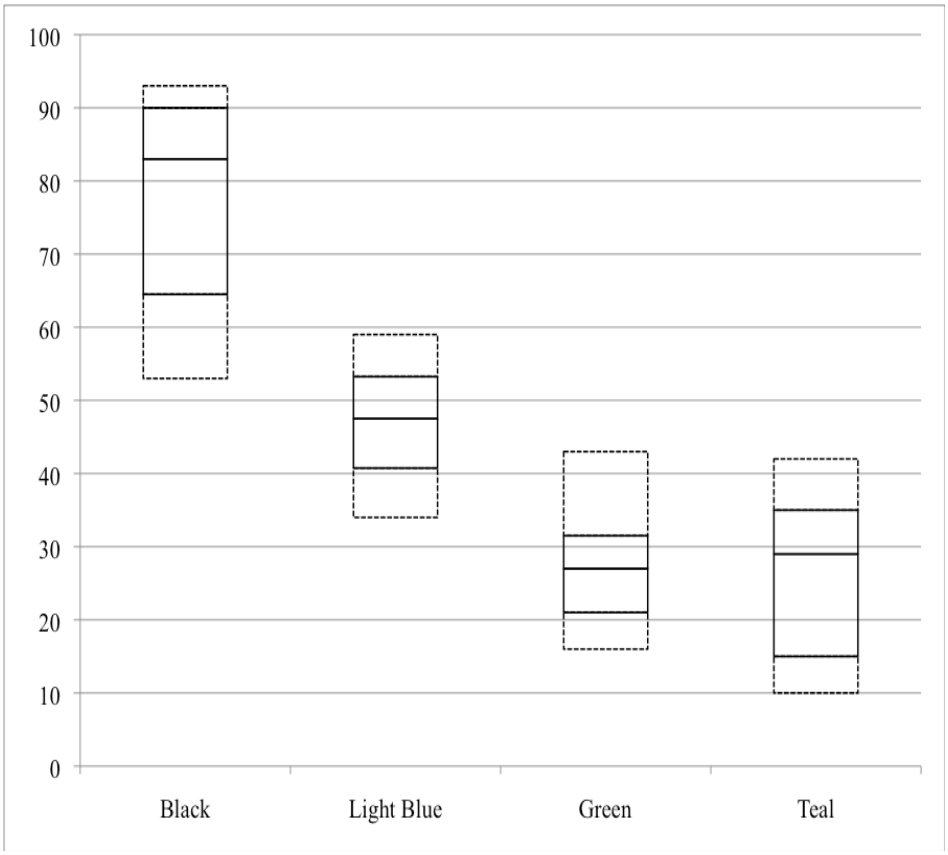


Figure 4.44 Box plot showing medians of observed instances of foraging. Y-axis indicates the number of times individuals were observed foraging.

Table 4.34 Results of comparisons of group feeding observations between all four study groups.

Feeding Incidents	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.800	0.0017	Y	Y
Black vs. Light Blue	12.600	0.0004	Y	Y
Black vs. Teal	3.630	0.0567	N	N
Green vs. Light Blue	7.088	0.0078	Y	Y
Green vs. Teal	0.339	0.5604	N	N
Light Blue vs. Teal	2.789	0.0949	N	N

Table 4.35 Results of comparisons of group foraging observations between all four study groups.

Foraging Incidents	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	9.800	0.0017	Y	Y
Black vs. Light Blue	10.587	0.0011	Y	Y
Black vs. Teal	11.118	0.0009	Y	Y
Green vs. Light Blue	9.779	0.0018	Y	Y
Green vs. Teal	0.137	0.7110	N	N
Light Blue vs. Teal	11.395	0.0007	Y	Y

Several strong differences are apparent in comparing time groups spent feeding. Black Group spent significantly more time feeding than both Green Group and Light Blue Group. Green Group also fed significantly more than Light Blue. Teal, notably, overlaps considerably in its range of medians, showing more variability than the other groups. Black Group and Teal Group had similar feeding times. Interestingly, groups in the Reserve approach, but do not reach significance.

In terms of foraging results, the Non-Reserve Groups Black and Light Blue, each show that they spent significantly more time foraging than the Reserve Groups when compared group to group. Black Group spends significantly more time foraging than each of the other groups. Following Black, Light Blue is significantly higher in its time spent foraging than both Teal and Green. Comparisons between Teal and Green Groups show no significant difference in foraging time. These significant differences are also clear when Non-Reserve and Reserve Groups are pooled to compare foraging strategy ($p<.01$) (Figure 4.45 and Table 4.36).

Table 4.36 Results of comparisons of foraging observations between pooled Reserve and Non-Reserve Groups.

Variable	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% significance level?	Reject H_0 at 5% significance level?
Forage	21.645	0.0001	Y	Y

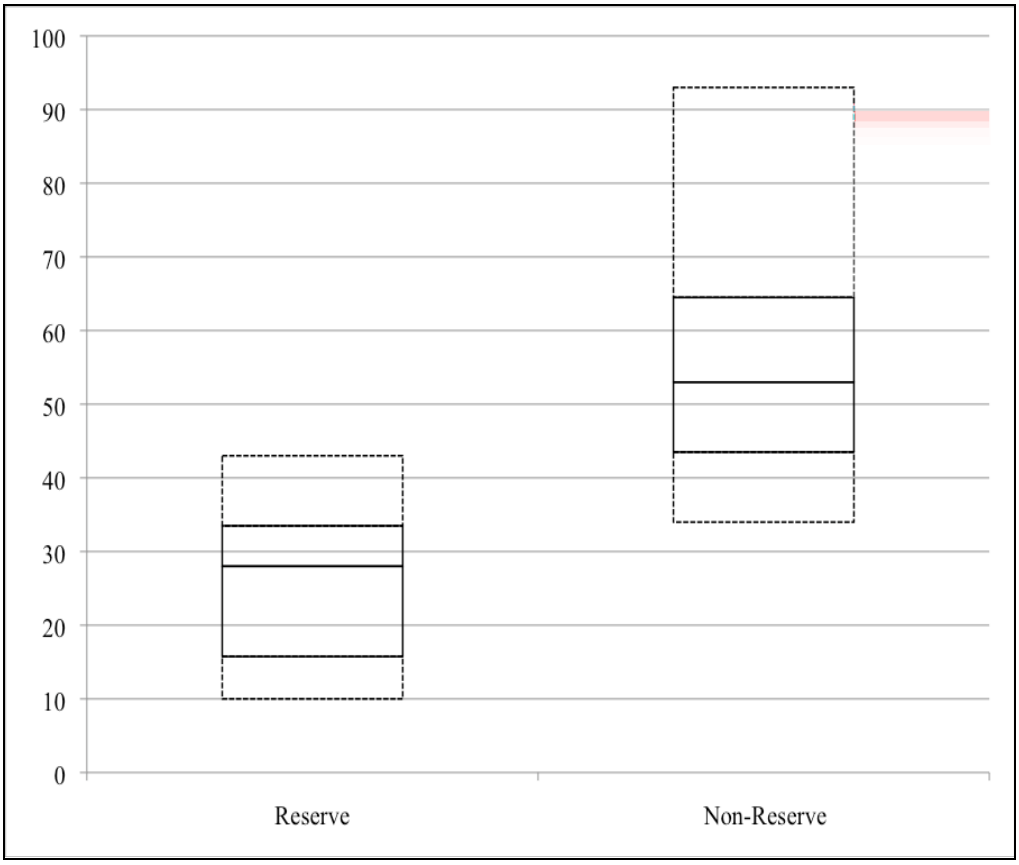


Figure 4.45 Box plot showing medians of observed instances of foraging for Reserve and Non-Reserve Groups. Y-axis indicates the number of times individuals were observed foraging.

4.5.2 Differences among Males and Females in Feeding and Foraging

Males in all four groups showed several important differences in time spent feeding (Table 4.37, Figure 4.46). Males in Black Group spent more time feeding than males in each of the other groups. In terms of results between the Reserve and Non-Reserve Groups, Green

Group males fed significantly more than males in Light Blue. Comparisons between Green and Teal males showed few differences, as did comparisons between males in Teal and Light Blue. In terms of foraging, similar differences were apparent between the groups (Table 4.38, Figure 4.47). Males in Black Group spent significantly more time foraging than did males in all other groups (K-W = 13.668, p-value = 0.0002). Light Blue Group spent significantly more time foraging than either of the Reserve Groups. When males were pooled into Reserve vs. Non-Reserve Groups, Non-Reserve males obviously spent significantly more time foraging than males inside the Reserve (p=0.0062, Figure 4.48).

Table 4.37 Results of comparisons of feeding observation comparisons between males in all groups.

Comparison of Male feeding times	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	5.000	0.0253	N	Y
Black vs. Light Blue	9.375	0.0022	Y	Y
Black vs. Teal	6.533	0.0106	N	Y
Green vs. Light Blue	5.600	0.0180	N	Y
Green vs. Teal	0.600	0.4386	N	N
Light Blue vs. Teal	0.026	0.8708	N	N

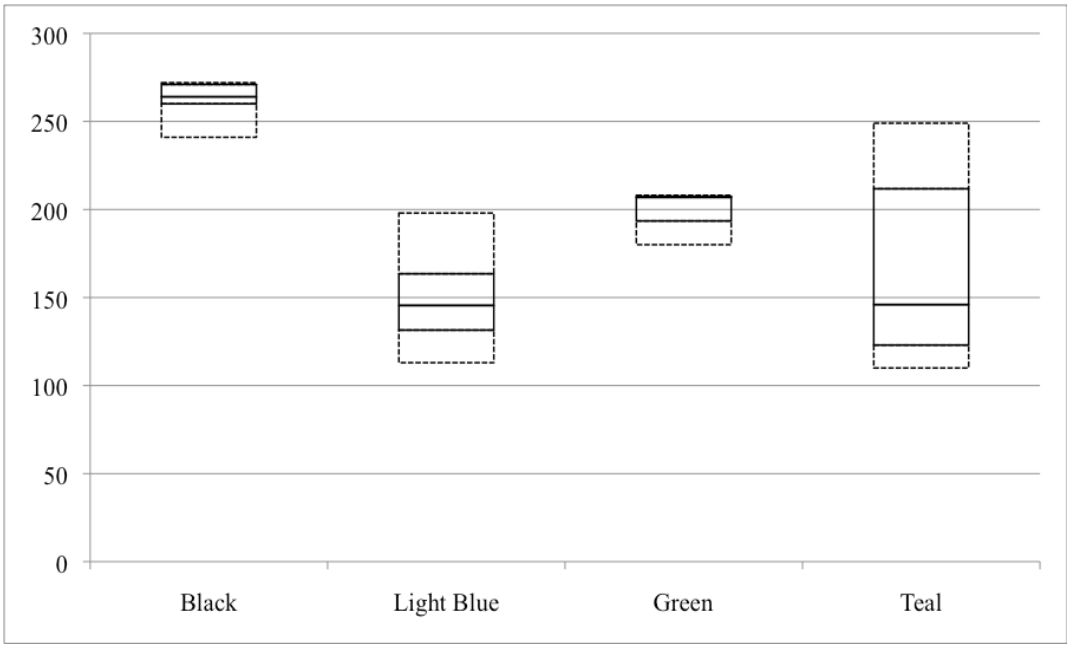


Figure 4.47 Box plot showing medians of observed instances of foraging males in each study group. Y-axis indicates the number of times individuals were observed foraging.

Table 4.38 Results of comparisons of foraging observation comparisons between males in all groups.

Comparison	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	5.000	0.0253	N	Y
Black vs. Light Blue	6.934	0.0085	Y	Y
Black vs. Teal	7.500	0.0062	Y	Y
Green vs. Light Blue	4.114	0.0425	N	Y
Green vs. Teal	1.667	0.1967	N	N
Light Blue vs. Teal	8.897	0.0029	Y	Y

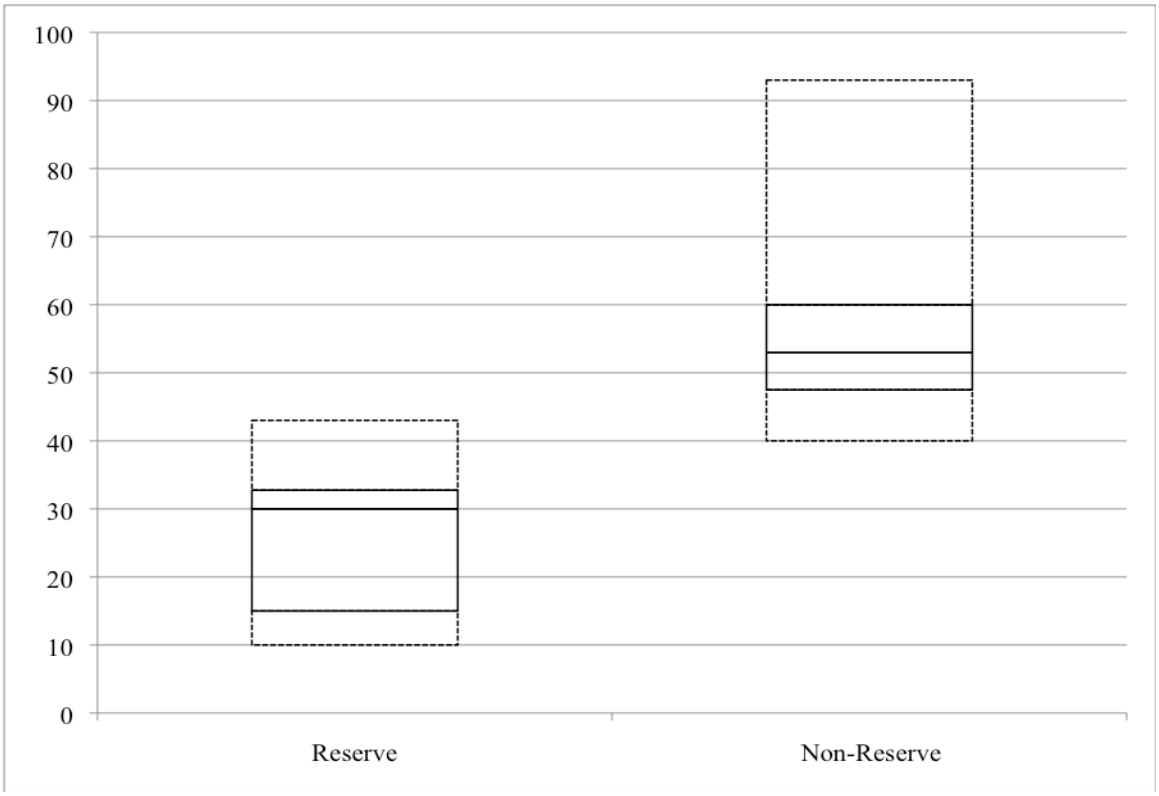


Figure 4.48 Box plot showing medians of observed instances of foraging males in each Reserve and Non-Reserve Groups. Y-axis indicates the number of times individuals were observed foraging.

In terms of females, very few differences were apparent when comparing feeding data between the four study groups. In fact, the only significant difference in these data showed females in Teal Group feeding more than females in Green Group (Table 4.39, Figure 4.49). As the box plots indicate, there is very little interindividual variability showing that female feeding times are a constant among these groups. For foraging, results indicated no differences in time spent foraging with the exception of Teal females foraging more than Green females (Table 4.40, Figure 4.50).

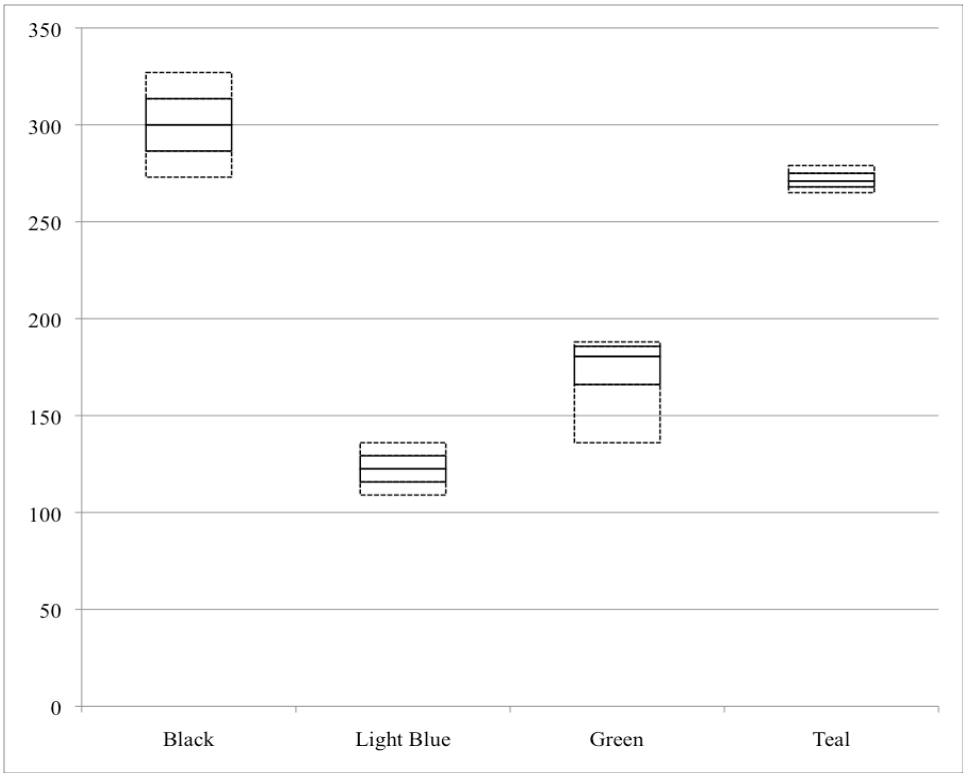


Figure 4.49 Box plot showing medians of observed instances of feeding females in each study group. Y-axis indicates the number of times individuals were observed feeding.

Table 4.39 Results of comparisons of feeding observation comparisons between females in all groups.

Feeding time comparison between the four groups	Value of K-W Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	3.429	0.0641	N	N
Black vs. Light Blue	2.400	0.1213	N	N
Black vs. Teal	1.333	0.2482	N	N
Green vs. Light Blue	2.625	0.1052	N	N
Green vs. Teal	4.500	0.0339	N	Y
Light Blue vs. Teal	3.000	0.0833	N	N

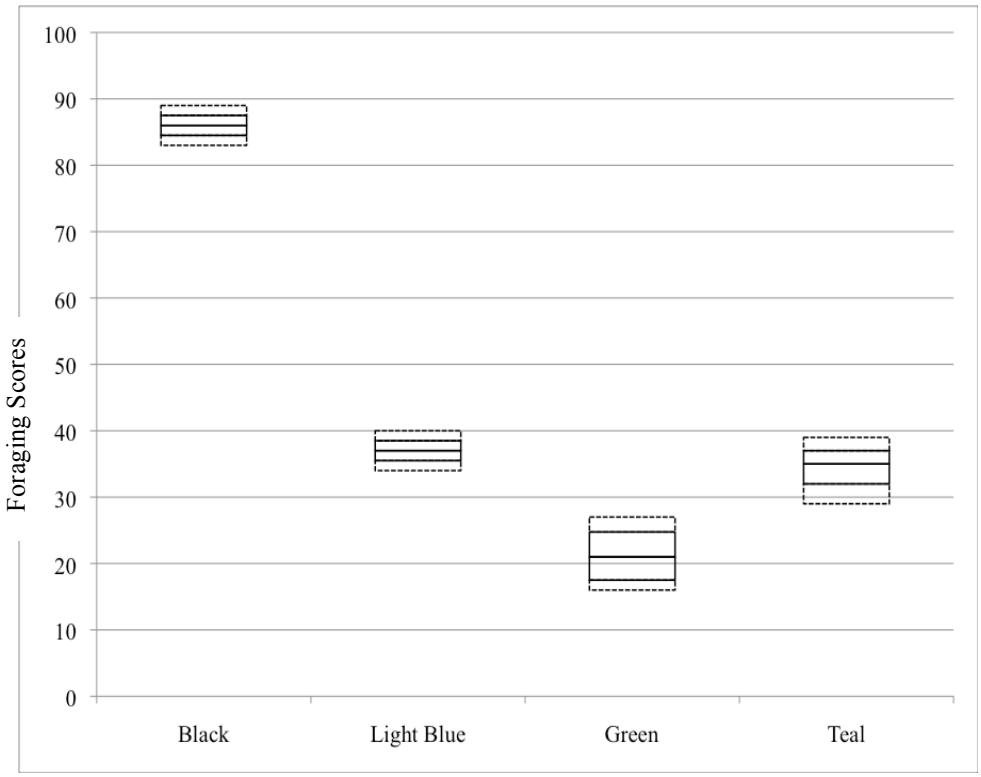


Figure 4.50 Box plot showing medians of observed instances of foraging females in each study group. Y-axis indicates the number of times individuals were observed foraging.

Table 4.40 Results of comparisons of foraging observation comparisons between females in all groups.

Comparison of foraging times between all four groups	Value of K-W Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	3.429	0.0641	N	N
Black vs. Light Blue	2.400	0.1213	N	N
Black vs. Teal	3.000	0.0833	N	N
Green vs. Light Blue	3.429	0.0641	N	N
Green vs. Teal	4.500	0.0339	N	Y
Light Blue vs. Teal	0.333	0.5637	N	N

4.6 Discussion

Anthropogenic habitat disturbance has exerted an influence on dietary composition and feeding behaviors of *L. catta* in and around Beza Mahafaly Special Reserve due to its effects on food availability, food quality, and habitat characteristics discussed in Chapter 3.

Dietary profiles in plant parts consumed are varied by recorded feeding instances, including 50-62% fruit consumption, 23-35% leaf consumption (both young and mature leaves), 3-7% flowers and flower buds, and 1-10% terrestrial herb consumption. Throughout the intense seasonality of this region of Madagascar, consumption of these different plant food types varies strongly with most groups increasing consumption of fruit in the wet season, and a dry season peak in leaf consumption. Overall, there are few differences in the groups' plant part consumption, but individual groups show significant differences in consumption of terrestrial herbs, with groups inside and closest to the Reserve relying on this resource. The same pattern is true for leaf consumption, and a strong component of these data are vine leaves that are present in more dense forest habitats: such as those present in, or close to, the Reserve. While there were differences among the four groups, these differences did not fall into a discrete and simple Reserve versus Non-Reserve dichotomy. Rather, these differences indicate a clear buffer effect from the Reserve that influenced how Black Group fed and foraged. Because of this group's close proximity to the Reserve, they experience fewer challenges than Light Blue Group, which appears to be in a more degraded habitat than Black Group.

During different months, while there are relatively few differences, it is important to note which plant parts become the focus for the various groups. For instance, during the rainy season, Non-Reserve Groups focused primarily on fruits, whereas groups inside BMSR consumed more leaves – both young and mature. As the dry season began in April, Non-Reserve Groups focused more on fruit and flowers, while Reserve Groups were again relying on young leaves. In fact, when groups are pooled together, these are the only monthly differences in consumption.

When considering the same groups' dietary profiles in terms of plant species consumed, a different picture emerges. When each group is considered individually, no clear pattern emerges

with the exception of Green Group consuming more of a fewer number of species. Non-Reserve Groups tended to distribute their consumption across more species, consuming smaller quantities from each of more species. Kily remains an important staple of each groups' diet. The most notable species that are different between the groups are terrestrial herbs (almost absent in Light Blue's diet) and tratraborondreo (*Grewia leucophylla*), which is nearly absent in the Reserve Groups' diet. Overall, it appears that groups tend to diversify their diets more in the wet season, and then rely on the same resources during the dry season. Green and Teal relied on a fewer number of species for the majority of their diet. This appears to signify that in more marginal habitats, *L. catta* is able to diversify its diet and exploit foods that might not be their primary choice. *L. catta* inside the Reserve appears to exploit resources that are available year round in a more consistent pattern. Non-Reserve Groups, perhaps because of a less predictable, consistent supply, tend to vary their species consumption more readily. Notably, Black Group's herb and fruit consumption indicates that they may be buffered by their proximity to the Reserve. As discussed in Chapter 3, their habitat just south of the Reserve appears to have several key resources that indicate it may be a valuable habitat to include in a Reserve expansion. These results indicate while Reserve Groups have access to thick, gallery forests containing a wealth of herbs and vines, groups in unprotected areas also have a variety of resources that are readily exploited by this species.

These differences are consistent with the differences observed in foraging and feeding. Non-Reserve Groups spend significantly more time foraging than groups in the Reserve. These differences are not as pronounced when examining actual feeding frequencies. It appears that groups outside the Reserve spend more energy and time searching for food than groups inside. This is consistent, and perhaps indicative, with their wider repertoire of species consumed during

the study year. The groups outside the Reserve may not be as familiar with the food source or may be forced to spend more time finding ripe or edible plant parts in each of the species they focus on. Perhaps food resources inside the Reserve are more predictable, allowing those groups to focus on familiar species. Finally, Non-Reserve males tended to spend more time feeding and foraging, while the same pattern did not hold true for females. It is possible that female dominance may reduce habitat effects so there are very few differences among Reserve and Non-Reserve females.

Further analyses of the chemical characteristics of each species consumed and body masses of individuals in each group will be necessary to fully understand the consequences of these dietary strategies and their implications for population viability. Groups inside the Reserve tended to consume the leaves of terrestrial herbs and lianas, even when other foods were available. In fact, it appears that these groups were using the herbs and vines as a staple resource, relying on it during the wet season when Non-Reserve Groups focus more on fruits. The fact that Reserve Groups focused on these terrestrial herbs and vines, when the species that other groups rely on are available, suggests that these leaves are higher quality and a preferred food. Or, perhaps *L. catta* tends to feed on what is most available in large patches. Groups outside of the Reserve gravitated toward the large stands of fruiting *Tallinella grevia*, *Grewia leucophylla*, or *Grewia grevei* fruit trees. Inside the more dense forest of the Reserve, herbs and vines were available in large patches, while for Green Group in particular, large stands of the other species are not present in the dense regions of the gallery forest. This might be a strategy for this opportunistic omnivore to avoid more competition between individuals and still acquire the nutrients and quantity they require. At present, all groups seem to be reproducing at similar rates. Birth rates during the study period between the habitats were quite similar, however,

survival rates inside the Reserve were much higher (Chapter 7). This may indicate that the Non-Reserve Groups' strategy of diversifying their diet, and spending more time foraging is not a long-term option for population success.

Having a higher foraging rate per feeding success, spending more time on a wider variety of food species, may contribute to Non-Reserve Groups being energetically stressed relative to groups inside the Reserve. Populations and groups under stress are more vulnerable to predation, disease, injury, natural disasters, and increased parasite loads. Due to the stochastic nature of these potent threats, it is quite possible that none of them will manifest in the short time of a 9-month study. However, groups outside the Reserve encountered significantly more feral dogs and cats than those inside the Reserve (Chapter 7).

Overall, it is difficult to assess what is normal for a season following a devastating cyclone. Groups inside the Reserve might have been exploiting a fallback food (herbs and vines) because kily trees were not producing as robustly as in a non-devastating cyclone year. In fact, previous studies have shown that groups inside the Reserve focus on more species than I observed during the study period (Simmen et al. 2006). It is possible that the cyclone disproportionately altered resources in the Reserve. Groups outside the Reserve, possibly more behaviorally adapted to a wider variety of resources, were able to target a wider variety of species more adeptly than groups inside the Reserve that are accustomed to a highly predictable and abundant resource such as *Tamarindus indica*. Interestingly, Loudon (2009) found that *L. catta* inside the Reserve harbored higher ectoparasite loads than groups outside the Reserve.

The power of generalizing these results to other primate species is limited because these types of data are inherently species and site specific. As more studies investigate how primates negotiate disturbed habitats and the effects of stochastic events, patterns and processes of

adaptability might emerge. One important result, however, that has been noted in another study of Malagasy primates inhabiting fragments is the reliance of groups on a seemingly insignificant resource, like the herb and vine patches used by Reserve Groups at Beza. Irwin (2006) noted that two *Propithecus diadema* groups residing in fragments relied significantly on a mistletoe plant. Indeed, Irwin deemed the plant a keystone resource for that population. It will be important in future studies to further detail and quantify the less obvious food categories in phenological and botanical inventories to fully understand how primates use these resources in addition to fruits, leaves, and flowers of larger plants. These strategies will allow researchers and conservation managers to make informed decisions regarding conservation strategies of populations and their survival in compromised habitats.

CHAPTER 5

EFFECTS OF ANTHROPOGENICALLY ALTERED FOREST ON *LEMUR CATTA*: SPATIAL ECOLOGY

5.1 Introduction

5.1.1 Anthropogenically Altered Forests: Habitat Loss and Conversion and Species Extinctions.

The destruction and conversion of primary primate habitat, and the accompanying loss, has been deemed one of the chief threats to biodiversity throughout the world (Cuaròn 2000). The dominant types of loss and modification are currently directly related to human activities. Scientists argue that it is critical to understand the processes of anthropogenic habitat disturbance in order to at least mitigate, if not eliminate, the negative changes (Laurance and Bierregaard 1997). In addition, before we can mitigate and eliminate these changes, we first must understand what types of responses they evoke in wildlife species. Quantitatively, it is relatively simple and useful to monitor the overall loss of habitat through remote sensing of both the area of habitat remaining and its spatial relationship within the landscape (Green and Sussman 1990, Irwin et al. 2005). Indeed, these methods make it possible in some discrete instances to predict the loss of species by quantifying the area of habitat that has been significantly altered and is no longer ecologically viable for wildlife (Cowlishaw 1999, Ganzhorn et al. 2003). Whereas this larger scale approach is useful for determining conservation priorities, it fails, however, to identify which taxa may be more vulnerable or which ecological processes and feedback mechanisms are pushing some taxa toward extinction (Irwin 2006). Finally, the larger scale approach also ignores how the remaining landscape configuration continues to add to biodiversity losses, a known occurrence in altered landscapes (Laurance et al. 2002).

As discussed in Chapter One, for wildlife inhabiting anthropogenically altered forests, there are several challenges that can be broadly grouped into the three categories mentioned above: proximate anthropogenic effects, degraded habitat variables and unsuitability of habitat, and the effects of landscape level changes. Particularly potent and dramatic are the direct effects of hunting, disease, and introduced predators on endemic populations. These are proximate factors that act quickly to eliminate individuals and may drastically reduce population size. On a longer time scale, the second category includes alterations to a habitat and its resource base. Research has shown that while it appears superficially to be less devastating than the outright denuding of forest land (i.e. fewer forested acres are converted to non-forested land), fragmentation and degradation is more subtle and insidious (Sechrest and Brooks 2002). Furthermore, when parts, or aspects, of the natural environment are removed or altered (extractive processes), these actions incur differential mortality of the historic ecology patterns. As a consequence, the habitat is less suitable for some organisms that have evolved under the pressures of an undegraded environment. Many human processes and activities contribute to habitat degradation including heavy human or livestock usages, extraction of resources, crop irrigation, and fire suppression, and conversion to agriculture (Sechrest and Brooks 2002). Commonly, these extractive and anthropogenic driven processes drive the degradation process further into habitat fragmentation. Degraded habitat variables and unsuitable habitat may inhibit wildlife population success or persistence, or create behavioral and ecological changes in response to changes in the habitat. The third category affecting wildlife in anthropogenically altered habitats are the landscape level effects and changes. These effects act on populations on the longest time scale. They affect population viability through limiting critical processes such as

dispersal, and increasing the predation risk for individuals traveling through exposed matrix habitats.

Variation is a consistent theme in the research literature examining the ability among species to survive and exist in anthropogenically altered habitats is (Chiarello and de Melo 2001, Ganzhorn et al. 2000ab, Ganzhorn et al. 2003, Gilbert and Setz 2001, Onderdonk and Chapman 2000, Tutin et al. 1997, Umapathy and Kumar 2000a). In the vast majority of studies, the variation is so extensive that there are no clear ecological variables such as body size, social organization, locomotor pattern, home range that can be definitively correlated to the variation in responses (some positive, some negative, and some seemingly neutral) of wildlife to habitat alterations.

Indeed, several comprehensive studies examining the probability of extinction for mammalian species assemblages in Madagascar illustrated that extinction proneness in fragments is consistent, and disturbed and fragmented landscapes are highly nested (Ganzhorn et al., 2000a,b, 2003). These authors estimated original population sizes in disturbed and fragmented habitats, based on current population densities. Results indicated that higher original population sizes tended to correlate with a greater chance of population survival and success. As previous discussion has indicated, species varied in their response to disturbance and fragmentation and this variation was not explained with the nested subset theory. This theory is an extension of the species-area relationship component of Island Biogeography Theory and its premise holds that species-poor small islands (or disturbed habitats) should support faunal assemblages that are subsets of larger islands (or continuous, undisturbed habitats) (Lindenmayer and Frank 2002). However, population density in continuous habitats may not be able to predict species extinction

proneness in disturbed forests: disturbed forests' characteristics may severely change a habitat's resource base and its carrying capacity.

As has been shown with primates in numerous studies, fragment area (or the area of disturbed forests) is not usually a significant indicator of species persistence in fragments and disturbed forests. For example, in Ranomafana, a comprehensive study examining lemur species assemblages in fragments illustrated the presence of nested subsets in fragments (Deghan 2003). Specifically, smaller fragments contained some of the same lemur species as were present in continuous habitats. However, neither fragment area or lemur species' body mass, relatively simple measures of species characteristics, are predictors of lemur species richness in fragmented and disturbed habitats (Deghan 2003). What is likely to have more predictive power to assess species persistence in altered landscapes are behavioral plasticity and flexibility, and quantitative measures of species requirements and resources available in altered habitats (Irwin 2006). These more dynamic variables, while more challenging to capture, may be more significant in assessing species population persistence that more static variables such as body weight and forest fragment area.

Capturing these intricate variables of resource availability throughout seasons, feeding patterns, and forest structure requires long-term ecological study. A thorough understanding of how the effects of anthropogenic habitat alteration affect the core of populations will promote valuable conservation management practices and an understanding of population dynamics in an ecological framework. Moreover, adding to the work of primate researchers examining the obvious abundance of variation in primates ability to exist in altered habitats will eventually lend clarity to the sea of inadequate predictive power conservationists are currently equipped with. A better understanding of the effects of anthropogenically altered habitats on ring-tailed lemur

feeding ecology will provide significant information for the management of this species at a landscape level, especially as it pertains to the protected and unprotected habitats in the Beza Mahafaly region. Further, feeding ecology is a natural foundation for examining less resource intense behavioral ecological variables such as activity patterns, social behavior, and spatial ecology. Finally, comparing populations with different ecological pressures and habitats, are relevant to furthering socioecological theory in general.

5.1.2 Spatial ecology and altered habitats

Spatial ecology refers to the examination and understanding of the patterns of habitat use and their consequences (Collinge 2001). Spatial heterogeneity, or homogeneity, of both populations and communities are an integral component of larger scale ecological topics such as adaptation, succession, competition, parasitism and disease (Perry et al. 2002). When examining the effects of altered habitats on a population, there are several ways in which the spatial alteration of traditional, unaltered, and continuous forest habitat may impact a species' spatial ecology. Group density within a given habitat may increase as the result of groups being condensed into a smaller habitable area. For instance, if a species relies on certain trees in its home range for sleeping sites, then groups will come into closer contact with each other to maintain proximity to a limited resource. Behaviorally, species that are dependent on larger groups sizes to reduce predation risk, will have an increased rate of close proximity interactions with conspecifics, and intergroup encounters. Resource distribution and abundance may also be affected and have consequences for a population and its community. First, carrying capacity may, in fact, increase or decrease depending on how habitat alterations effect a species' dietary needs, availability of resources (perhaps an introduced species alleviates demand for native diets), and group size and ranging patterns may adjust (increasing or decreasing) as a

consequence. Second, it has been well documented how intimately connected primate ranging patterns are to the density and distribution of food resources (Kaplin 2001, Marsh 1981, Milton 1980, Remis 1997, Singleton and van Schaik 2001, Warren and Crompton 1997), as such, species may use their habitat differently which will, in turn, affect ranging patterns. Finally, if individuals in a group are affected by feeding competition, a major determinant of group living (Barton et al. 1996, Chapman and Chapman 2000, Janson and Goldsmith 1995), optimum group size and, in turn, ranging patterns, may also experience change.

For primates, spatial ecology is primarily the examination of patterns in home range size, habitat use, and population density (group size, intergroup spacing). In anthropogenically altered habitats, there are a few well-studied primate populations that have data on both population density and home range size. In India, MeNon and Poirer (1996) recorded a 35 ha smaller home range size for lion-tail macaques in forest fragments compared to those in a nearby continuous forest habitat. Similarly, Howler monkey home range size in altered habitats has often been found to be extremely small, settling in forest fragments that are 10 times smaller than nearby continuous forests (Estrada and Coates-Estrada 1996, Estrada et al. 1999, 2002). Black and white colobus (*Colobus guereza*) had an approximately 53% reduction in home range size in forest fragments near Kibale National Park, Uganda (Oates 1977, Onderdonk and Chapman 2000). These colobus also compensated for their reduction in home range size with a smaller group size. In other cases, group size has actually increased in altered habitats that are not as severe a reduction (Menon and Poirier 2006, Singh et al. 2002, Umapathy and Kumar 2000a). Interestingly, a pattern emerges when comparing species that appear able to persist in anthropogenically altered habitats and those that eventually do not: species that do not tolerate habitat alterations and degradation or fragments tend to harbor less dense populations. On the

other hand, species that have been shown to persist in fragmented and anthropogenically degraded habitats exist as higher density populations in the altered forests (Estrada et al. 1999, 2002, Rodriguez-Toledo et al. 2003, Singh et al. 2002, Tutin et al. 1997). There appear to be some species that can adjust to fragmented and altered habitats with a reduction in home range size and an increase in population density to compensate for the effects of habitat alterations.

Movement and habitat use patterns in altered and fragmented habitats have not been comprehensively studied to date (Irwin 2006). For the few studies available, howlers were shown to compensate for small fragment size with longer daily movements even though one would expect that ranging patterns would correlate with fragment size (Bicca-Marquez 2003). Indeed, in another example, *Macaca silenus* that inhabitated a small forest fragment surrounded by agricultural fields regularly ranged widely into the croplands and traveled terrestrially to maneuver the denuded landscape (Sing et al. 2001). Similarly, sifakas resident in forest fragments in eastern Madagascar experienced greatly reduced home ranges, but only moderately reduced daily path lengths (Irwin 2006). From these examples, one might conclude that resource distribution is the predominant variable for determining ranging patterns and length. However, with so few studies to draw from, it is premature to evaluate how habitat affects ranging and resource use.

5.1.3 Social structure and spatial ecology of *Lemur catta*

As with many species, population density and home range of ring-tailed lemur varies greatly with habitat type. At both Berenty and BMSR, where the Reserves contain distinct and adjacent habitats, *L. catta* density varies according to these distinct types. In the gallery forests, density ranges up to 500/km^2 at Berenty and 137/km^2 at Beza (Jolly et al. 2006, Sussman 1991). Groups to the north and south of BMSR, in unprotected areas, are half the density of the

population inside the protected area (Whitelaw and Sauther 2003). In drier areas to the south and mountainous habitats in Andringitra, population density is much lower: 8-64/km^2 in the south and 22/km^2 in the Andringitra (Raharivololona and Ranaivosoa 2000, Rakotoarisoa 2000).

Group sizes also tend to vary between sites and habitat types. For instance, at Berenty, the smallest groups (average 8.9 individuals) tend to reside in drier forests and the larger groups (13.9 individuals) in the tourist areas of this private Reserve (Jolly et al. 2002, Koyama et al. 2002). At BMSR, average group size within the Reserve is 8.71. Outside the Reserve, group sizes tend to average slightly larger, 14.33.

Socially, ring-tailed lemur groups are composed of a core of adult females, their offspring, one or several central males, and peripheral males (Gould 1997, 2006, Jolly 1966, Sauther, 1992, Sauther et al. 1999, Sussman 1992). Some groups may contain more than one resident matriline, and one will be dominant to the other (Nakamichi and Koyama 1997, Sauther 1992, Taylor and Sussman 1985). Several evictions of subordinate matrilines (core females and their offspring) have been recorded in captive and wild populations (Gould et al. 2003, Jolly et al. 2002, Koyama 1991, Koyama et al. 2002, Sussman 1991, Taylor and Sussman 1985). These evictions, along with larger group sizes of 15-20 individuals, can result in group fissions (Jolly et al. 2002, Gould et al. 2003, Sauther and Cuozzo, unpublished data; Whitelaw pers. obs., Sussman 1991).

Social structure in *L, catta* has been characterized as multi-male, multi-female (Jolly 1966). Unique among most lemur species, females are socially dominant over males, exhibit female feeding priority and true female dominance (Jolly 1966). Furthermore, females bear the majority of range defense events between neighboring groups (Ichino and Koyama 2006). Matrilines are relatively stable over time and remain stable in their home range except for

relatively rare, major social change events such as fission, eviction, and dissolution when groups become very small (Gould 2006, Ichino and Koyama 2006).

Similar to both population density and group size, home range size also varies with habitat type. For instance, in gallery forests at Berenty, home ranges vary from 3.95 ha to 16.7 ha whereas in drier habitats at Berenty they exhibit home ranges of 12-25 ha (Jolly et al. 1993). BMSR, a similar pattern emerges: gallery forests contain groups with 17 ha average home ranges and western, drier habitats contain groups with 32 ha average ranges (Sussman 1991). *L. catta* living at relatively high elevation in the Andringitra region are described as using vertical ranges between 1310m – 2360m and 1250m – 2040m (Goodman et al. 2006). Day ranges at each of the sites where data are available (Berenty, Ansirananomby, Andringitra) tend to be approximately 1000m (Goodman et al. 2006, Gould 2006, Jolly et al 1993, Sussman, 1972, 1999).

Due to *L. catta's* semi-terrestrial traveling behavior, they use a variety of habitats (Goodman et al. 2006). In gallery forests, terrestriality ranges from 3-75%, averaging 30%, and varying seasonally (Jolly 1966; Sauther 2002, Sussman 1971, 1977). True to this species "extremely adaptable primate" reputation (Gould 2006: 255), they are capable of ranging and dispersing across unforested habitats and matrices, hence, their landscape is unconstrained by gallery forest networks along the rivers of southern Madagascar (Goodman et al. 2006, Gould 2006). Despite this asset, populations have declined over the last half-century due to the anthropogenic devastation of the dry forests of Madagascar (Sussman et al. 2003).

It appears that local distribution and abundance of *L. catta*, are dependent more on habitat variables than phylogeny. Drier forests have lower density and group sizes and gallery forests contain denser populations and larger groups. This observation is key to understanding how

anthropogenically altered habitats will affect the long-term demography and success of *L. catta* populations.

5.1.4 Objectives

This chapter examines the impact of anthropogenically altered habitats on the spatial ecology of *Lemur catta* in and around BMSR. Specifically, I examine how anthropogenically altered habitats affect home range size, daily path length, frequency of travel, group cohesiveness and vertical habitat use. The answers to these questions allow for a better understanding of how this species utilizes habitats – both relatively undisturbed and increasingly altered. This knowledge allows conservation managers to effectively prioritize the habitats that are most suitable, and the most productive from the lemur's point of view. Additionally, this study, coupled with others like it, provides a significant contribution towards understanding how some primate species adapt behaviorally to challenging landscapes, whereas others fail. Most studies of lemurs and other primates in the wild have focused on and sought populations living in undisturbed landscapes. Currently, we know relatively little about how primates negotiate disturbed and altered habitats. Contributions to this knowledge gap will begin to expand our socioecological understanding of primates in the wild and provide benefits for conservation management of endangered primates.

5.2 Methods and Analysis

5.2.1 Data Analysis

Total sample size on which the analyses are based is almost 300 group follow days which encompass almost 800 hours of contact time. I collected GPS coordinates on each group follow day to describe each groups' daily path length; I used all collected points to calculate each groups' home range.

Home range sizes for each group were calculated using three methods: Minimum Convex Polygon (MCP), 95% fixed kernel, and 50% fixed kernel. The MCP method has the advantage of being relatively simple in that it provides the area described by the smallest convex polygon constructed to fit the set of point locations provided by the data set. The MCP's disadvantage is the tendency to overestimate home range size based on the inclusion of large, unutilized space.

Wildlife tends not to adhere to straight lines between points, instead adopting a more organic, needs-based approach to ranging. To provide a more realistic home range, I also used the fixed kernel method, which produces a more realistic home range polygon shape by modeling the home range with a probability variable (Worton 1989) and a smoother shape with a parameter described as '*h*' (Silverman 1986). The 95% kernel home range method illustrates the space (two-dimensional) in which 95% of the group's movement is predicted to be limited and the 50% kernel home range depicts the space in which 50% of the group's movement is predicted to be limited. I used the former method to estimate home range size and the latter to portray each groups' core area. These calculations were produced with the Animal Movement Analysis ArcView extension (v2.04; Hooge and Eichenlaub 1997).

I used a subset of the GPS data to calculate daily path lengths for each group. The criterion I used for inclusion was: the daily path length must be completely recorded by GPS, or reliably estimated if a portion was missed in the morning. Thirty-nine GPS data days were excluded for not containing enough reliable points. I calculated daily path length by connecting GPS locations sequentially throughout each day. Straight lines were used between all points, because long travel times and circuitous routes were noted specifically in anecdotal accompanying notes and multiple GPS points taken to ensure accurate portrayal of daily travels.

I calculated path lengths in two dimensions because height differences would be analyzed in another section. I used a Kruskal-Wallis ANOVA to compare differences between groups.

To compare patterns of vertical habitat use and terrestriality versus arboreality, I recorded the height of each individual during the 10 minute focal sample and the location of the group (terrestrial or arboreal) during the group scan. I used a Kruskal-Wallis ANOVA to test for significant differences in arboreal habitat use between the four study groups. Additionally, I collected data on group spread utilizing a laser range finder to determine how far individuals were from each other after each focal animal sample during the group scan. These group spread parameters included sitting close (sitting in contact), close (2-4 meters), medium (4-6 meters), far (6-12 meters), very far (>12 meters).

Similarly, I used a Kruskal-Wallis ANOVA to assess differences in traveling behavior, utilization of closed canopy and open canopy habitats, and the frequency of severely versus lightly disturbed habitat. I classified the current habitat that the lemurs were using the following categories, 1=less disturbed (Parcel 1), 5=more disturbed (fragmented, anthropogenically altered habitats). Degradation variables included evidence of tree cutting, presence of livestock feces, grazing, roads, crops, and severe deforestation.

5.3 Home Range

5.3.1 Home Range Size and Population Density

Home range size was reduced for Non-Reserve Groups relative to the Reserve Groups in all methods of calculating home range (Table 5.1). Reserve Groups occupied home ranges of 274-383 km^2 and Non-Reserve Groups ranged in areas from 204 km^2 to 223 km^2. The order from smallest to largest range size was: Light Blue, Black, Teal, and Green (Table 5.1; Figures 5.1a, 5.1b). This aspect also influenced population density among the groups with Non-Reserve

Group habitats featuring denser populations of lemurs relative to their Reserve counterparts (Table 5.5). It must be noted that these densities do not control for range overlap, and Reserve Groups tend to be close together. However, they might range farther to counteract group density.

Table 5.1 Home range size and Population Density for all groups.

Group	Home Range Size MCP	Home Range Size 95% Kernel (m^2)	Home Range Size 50% Kernel (m^2)	Habitat Status	Population Density Estimate (individ./km^2)
Black	223,276.5 m^2	178,233	47,651	Non-Reserve	40
Light Blue	204,383.5 m^2	186,665	48,950	Non-Reserve	58
Green	383,130 m^2	254,842	45,787	Reserve	26
Teal	274,264.5 m^2	248,087	57,172	Reserve	36

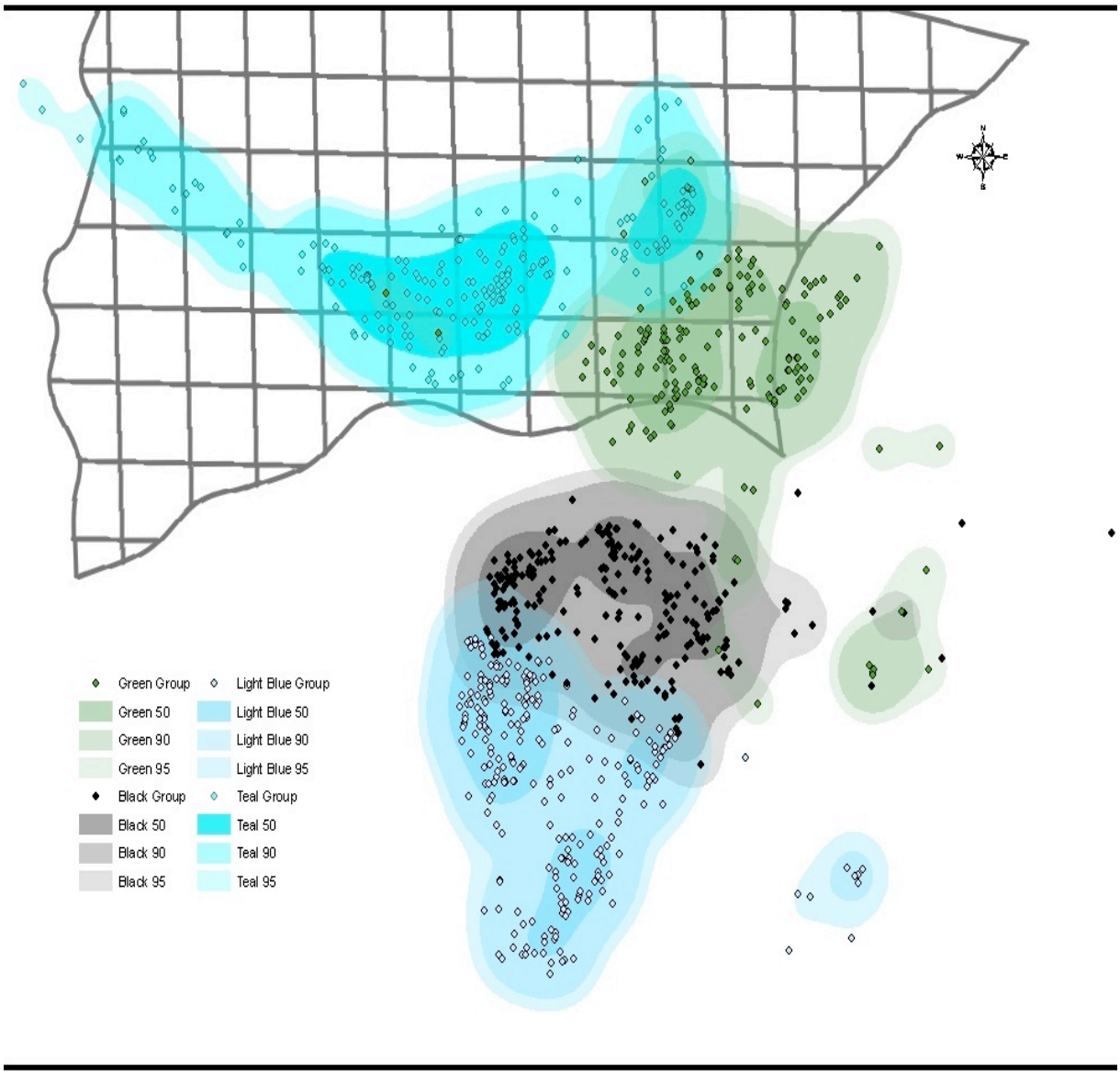


Figure 5.1a All groups' home and core kernel ranges overlayed with BMSR grid trail map.

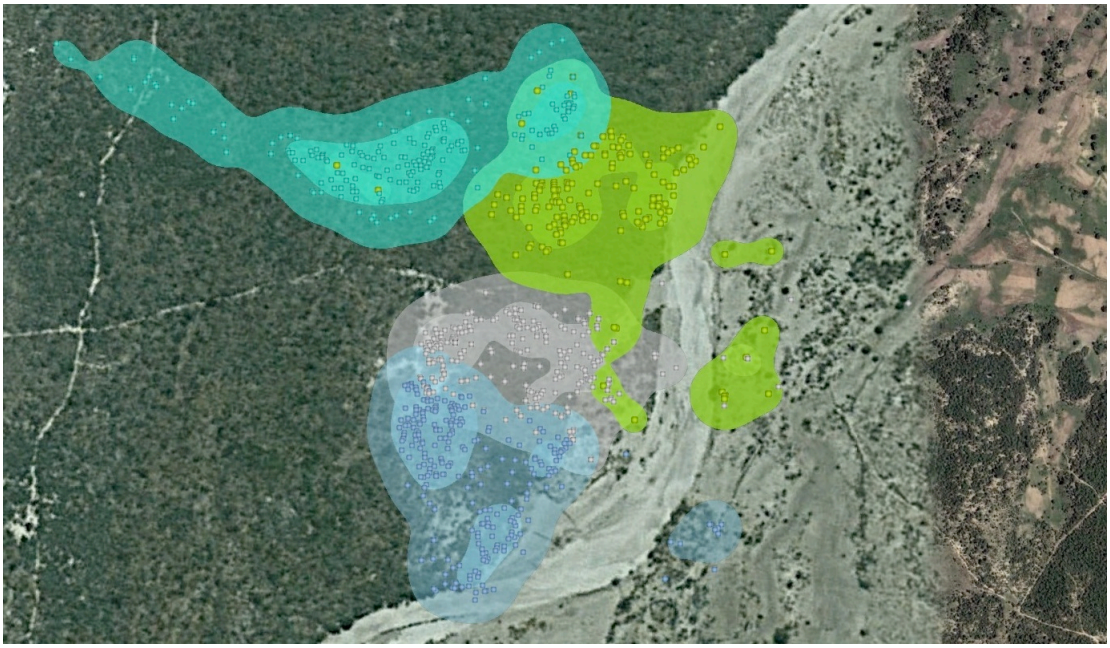


Figure 5.1b All groups' home and core range overlayed with satellite image of BMSR.

5.3.2 Home Range Configuration Relative to Landscape

Green and Teal (Reserve Groups) home ranges show a core range in the interior of the forest (Figures 5.1a, b). These groups do not have the challenge of heavily agricultural land bordering their ranges and they tend to occupy the forested areas in their ranging patterns. Similarly, both Black and Light Blue (Figures 5.1a, b) Groups maintain the majority of their ranging activity as far as possible from the heavily disturbed riverside deforested area. Black Group regularly accessed the 'finger fragment forest' which is the farthest eastern extension east of the gallery forest close to the river and just south of BMSR. In fact, Black and Light Blue Group regularly accessed resources along the edges of their ranges. These edge habitats were often centers of fruit production presumably because of abundant sun exposure due to thinning and deforestation for agriculture.

All groups, with the exception of Teal, occupied ranges bordering the Sakamena River. Furthermore, each river-bordering groups accessed resources on the opposite side of the River throughout the study period. These resources included: mangos, filo filo (*Azima tetracantha*), and kily (*Tamarindus indica*). Although reported in previous studies (LaFleur and Gould, 2009), they did not eat domesticated agricultural crops such as bageda (Convolvulaceae sp.) during this study period. These foods are usually exploited during the late dry season (July-August) and my study did not include these months. The cross-river resources were in extremely degraded areas with high human traffic, human settlements, and agricultural fields. As a consequence, domestic dogs were often present as the ring-tailed lemurs pursued these resources. Similar to the centers of fruit production along edge habitats in their ranges on the Reserve side of the Sakamena, cross-river habitats also had abundant sun exposure thus supporting abundant lemur resources that were also available in the Reserve such as *Tamarindus indica* and *Azima tetracantha*.

Green and Teal Groups came in contact with other collared groups ranging in and around BMSR: Red, Yellow, and Lavender. In contrast, Black and Light Blue Groups rarely came into contact with other collared groups. Only Black Group held intergroup encounters with Orange Group. Light Blue Group occasionally came into contact with an uncollared group to the south of their range.

5.4 Daily Ranging Patterns

Daily path length was longer for groups outside the Reserve than for those within (Table 5.2). Examination of each groups' averages indicate the following ranking of path length from longest to shortest: Black, Light Blue, Teal, and Green. Non-Reserve Groups have longer average and daily daily path lengths. (Table 5.3, Figure 5.2).

Table 5.2 Average and Median Daily Path Lengths for all groups.

Group	Average Daily Path Length (meters)	Median Daily Path Length (meters)
Black	628	491
Light Blue	447	463
Green	271	185
Teal	353	291

Table 5.3 Results of Kruskal-Wallis test comparing the median path length of all four study groups and Reserve versus Non-Reserve Groups.

Comparison of each groups' path length	Value of Kruskal-Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	15.213	0.0001	Y	Y
Black vs. Light Blue	1.426	0.2325	N	N
Black vs. Teal	6.287	0.0122	N	Y
Green vs. Light Blue	11.981	0.0005	Y	Y
Green vs. Teal	4.490	0.0341	N	Y
Light Blue vs. Teal	2.505	0.1135	N	N

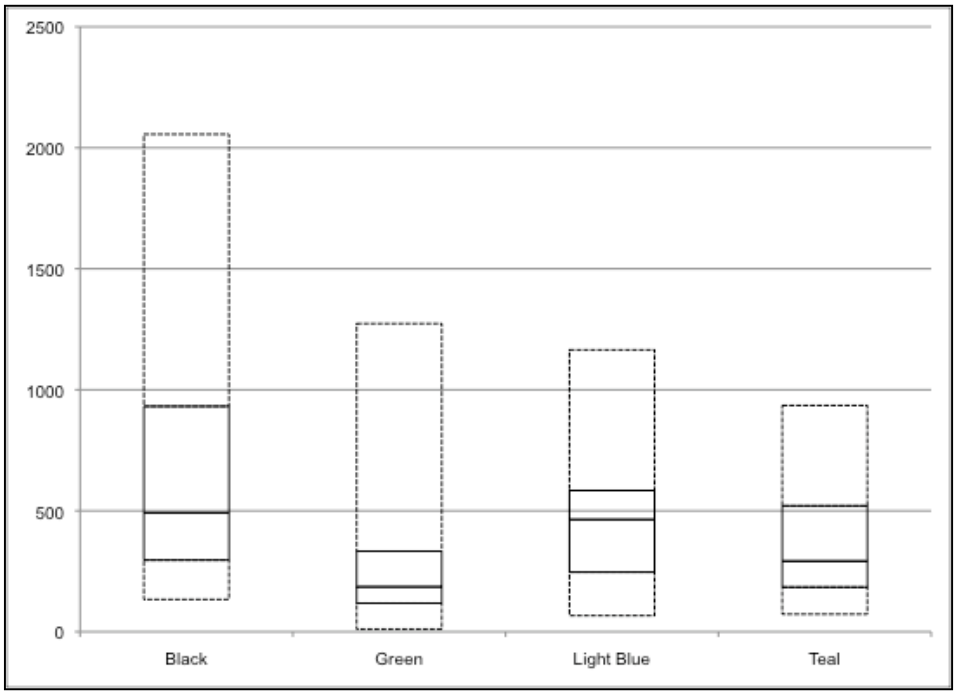


Figure 5.2 Boxplots of all four study groups' daily path lengths in meters.

When average daily path length is illustrated by month, seasonal variation is apparent (Figure 5.3). Daily path lengths are generally higher in months of higher precipitation (December, January, February, and March), and lower during drier months (October, November, April, May, and June). As the quantitative analysis indicates, Green and Teal Groups show consistently lower daily path lengths relative to the Non-Reserve Groups. Black Group shows a consistent, significantly higher path length. This may be due to their inclination to access cross-river resources such as *Azima tetracantha* and *Mangifera indica*.

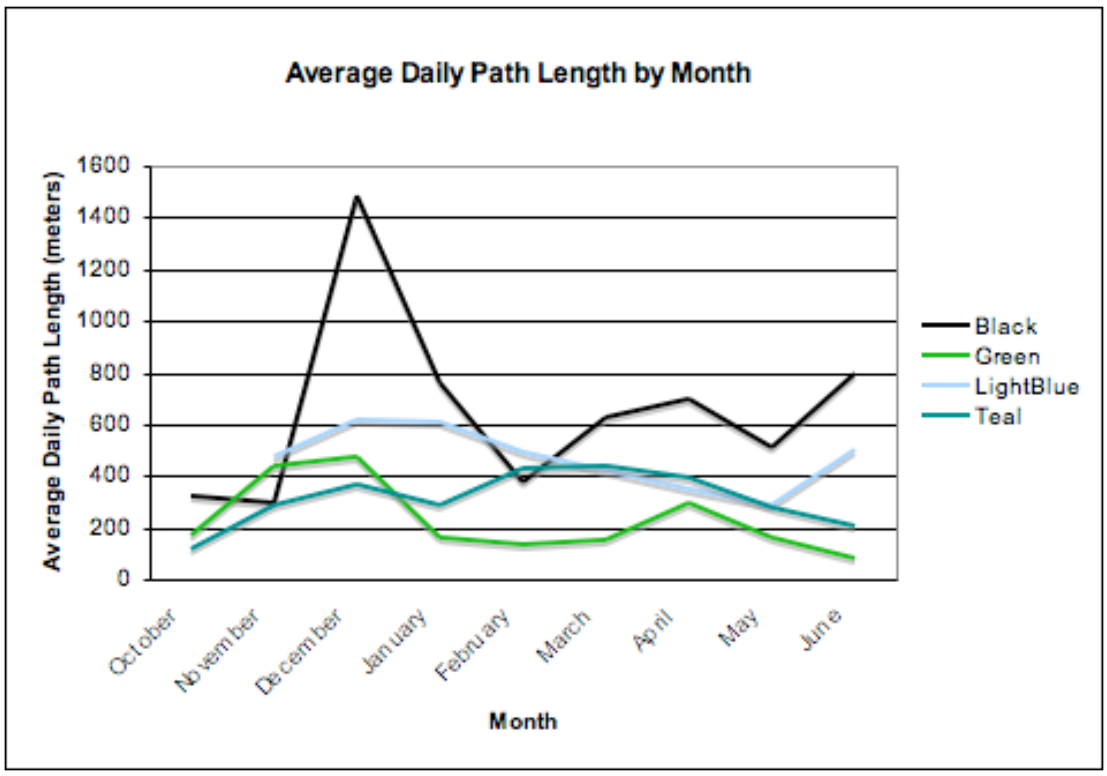


Figure 5.3 All four study groups' average daily path length by month.

5.5 Vertical Habitat Use

Because there are significant differences in the forest habitat structure of each groups' home range, one would expect these groups to show noteworthy differences in their patterns of vertical habitat use (Table 5.4, 5.5, Figure 5.4, 5.5). In fact, there are several important differences including Reserve Groups utilizing slightly higher median height zones (Reserve median: 6.0 m, Non-Reserve median: 4.0 m; Reserve average 6.2 m, Non-Reserve 5.0 m). Among the groups, Green Group ranked highest in median vertical height use (6.0 meters, average 6.8 meters), then Light Blue and Teal with the same median (5.0 meters; Light Blue average – 6.0 meters, Teal average 5.4 meters), and Black utilizing the lowest median vertical height (4.0 meters; average 4.0). Quantitatively, this ranking was significant (Table 5.4, Figure 5.5). Overall, vertical height use appears to be quite similar and the number of samples collected for this particular variable lends itself to creating a very sensitive statistical comparison. Teal

and Light Blue Groups appear to be the most similar; perhaps this is a symptom of their similar habitats (further away from the river and in drier, scrub forests).

Table 5.4 Average and median height use for each group.

Group	Average Daily Height Use Average (meters)	Median Daily Height Use Average (meters)
Black	4.0	4.0
Light Blue	6.0	5.0
Green	6.8	6.0
Teal	5.4	5.0

Table 5.5 Comparisons statistical analysis of median vertical height use between all four study groups and Reserve versus Non-Reserve Groups.

Comparison of vertical height use between all 4 study groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	986.412	0.0001	Y	Y
Black vs. Light Blue	418.775	0.0001	Y	Y
Black vs. Teal	235.828	0.0001	Y	Y
Green vs. Light Blue	96.436	0.0001	Y	Y
Green vs. Teal	151.575	0.0001	Y	Y
Light Blue vs. Teal	10.571	0.0011	Y	Y
Comparison of vertical height use between Reserve and Non-Reserve Groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H0 at 1% sig. level?**	**Reject H0 at 5% sig. level?**
Reserve vs. Non-Reserve	422.279	0.0001	Y	Y

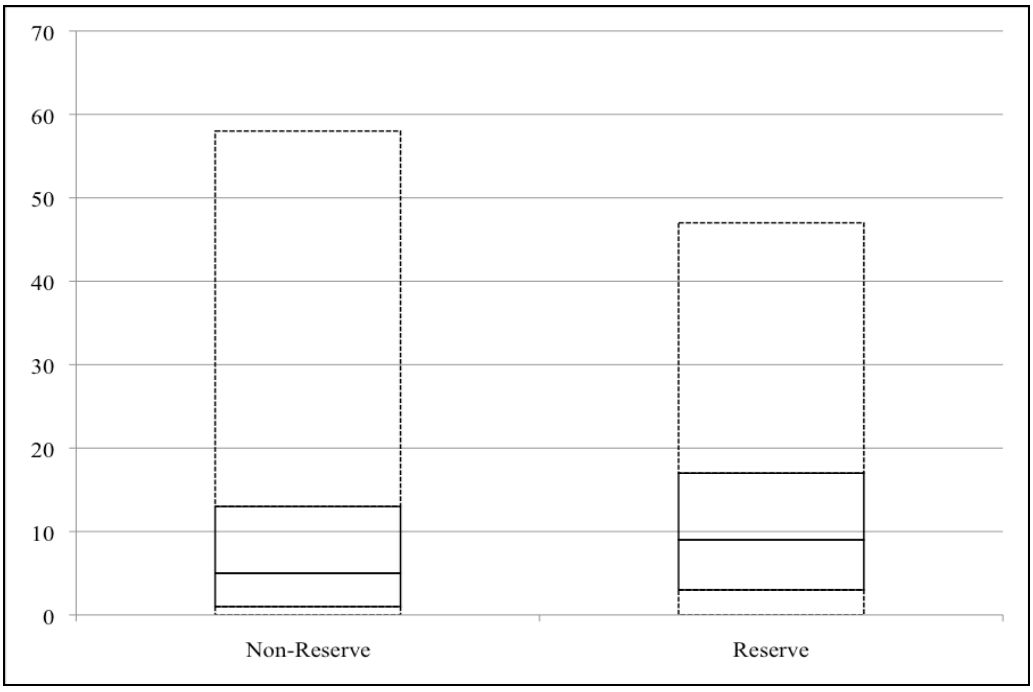


Figure 5.4 Boxplot comparison of vertical height use in Reserve versus Non-Reserve Groups. Y-axis indicates height in meters.

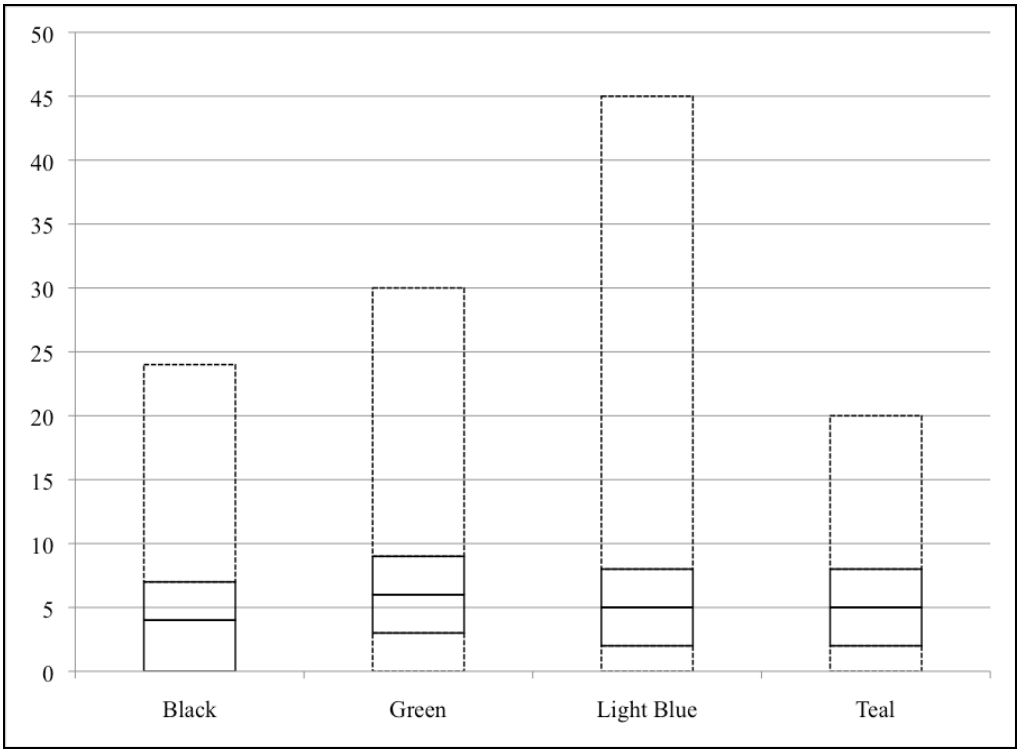


Figure 5.5 Boxplot comparison of vertical height use in all four study groups. Y- axis indicates height in meters.

When examining height use during feeding, the same pattern emerges. Light Blue and Teal have the same median (6.0 meters) and slightly different averages (Teal 5.6 m, Light Blue 6.6 m) and this variation does create a significant difference when these two groups are compared (Kruskall-Wallis test statistic: 45.678, $p<0.001$). Black Group remains the lowest in terms of vertical height use during feeding (median: 4.0 m, mean 4.8 m). Green Group, again, has the highest median and average vertical height usage during feeding (median: 7.0 m; average 7.1 m). As it was in the previous section, Reserve Groups consistently spend more time feeding at slightly higher levels (median: 6.0 m; mean 6.4 me) than Non-Reserve Groups (median 5.0 m; average 5.6 m). This result is interesting in light of the focus on herbs found in Reserve Groups, but may be highlighting their emphasis on vines and lianas for leaves that are mostly absent from Non-Reserve habitats.

5.6 Arboreality Among Groups

Overall, groups spent the vast majority of their time in the arboreal part of their habitats (78%) (Table 5.6, 5.7, Figure 5.6a,b). When these data were collected, I recorded whether the group was terrestrial or arboreal, therefore the choice of choosing the percentage of arboreal rather than terrestrial as the variable of interest is mathematically arbitrary; it does not change the significance of any results. For these analyses, I compare arboreality among the groups. Results indicate that aboreality is not strictly tied to habitat. Indeed, Green Group spent significantly more time in the trees than any of the other groups (Table 5.7; $p<0.05$, Figure 5.7). While not significant, Teal spent more time arboreally than either of the Non-Reserve Groups, and Light Blue is in the trees more than Black (Figure 5.7).

Table 5.6 Comparison of overall terrestrial and arboreal habitat use among groups.

	Terrestrial	Arboreal
Black	28.4%	71.6%
Light Blue	25.8%	74.2%
Green	12.5%	87.5%
Teal	20.0%	80.0%
Non-Reserve	23.4%	76.6%
Reserve	20.9%	79.1%
Total	22.0%	78.0%

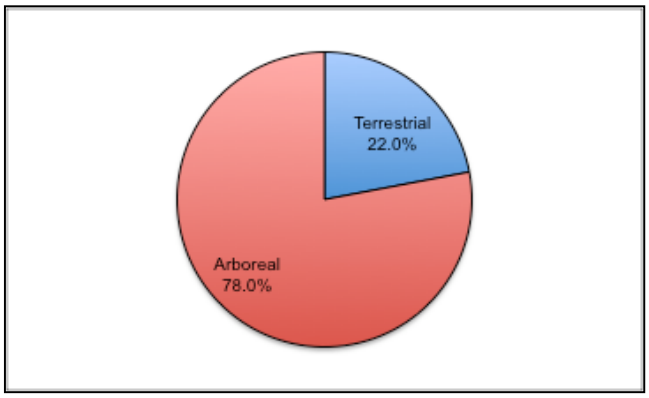


Figure 5.6a Overall arboreal versus terrestrial habitat use for all groups.

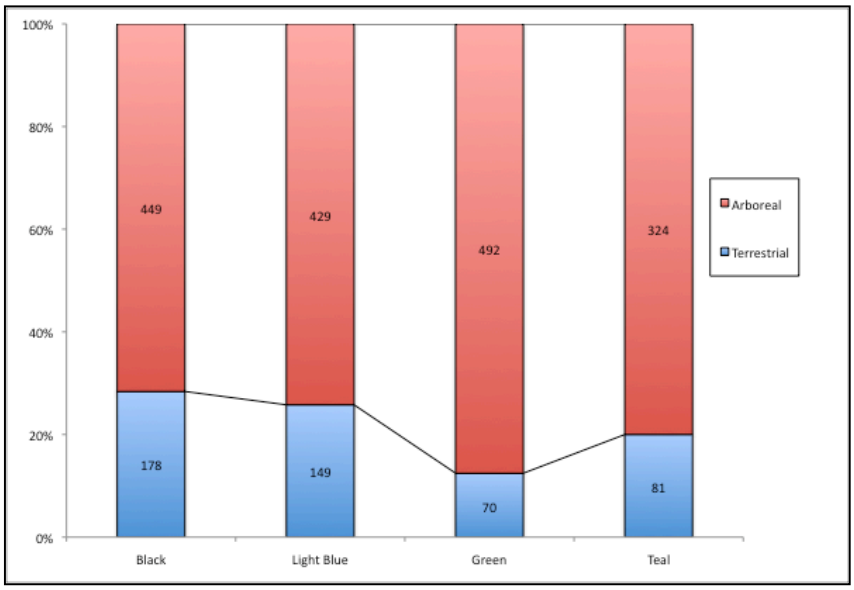


Figure 5.6b Percentage of arboreal versus terrestrial habitat use for each study group.

Table 5.7 Results for arboreal habitat use comparison among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of Arboreality between all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	9.832	0.0017	Y	Y
Black vs. Light Blue	0.755	0.3850	N	N
Black vs. Teal	1.473	0.2249	N	N
Green vs. Light Blue	6.695	0.0097	Y	Y
Green vs. Teal	4.354	0.0369	N	Y
Light Blue vs. Teal	0.276	0.5996	N	N

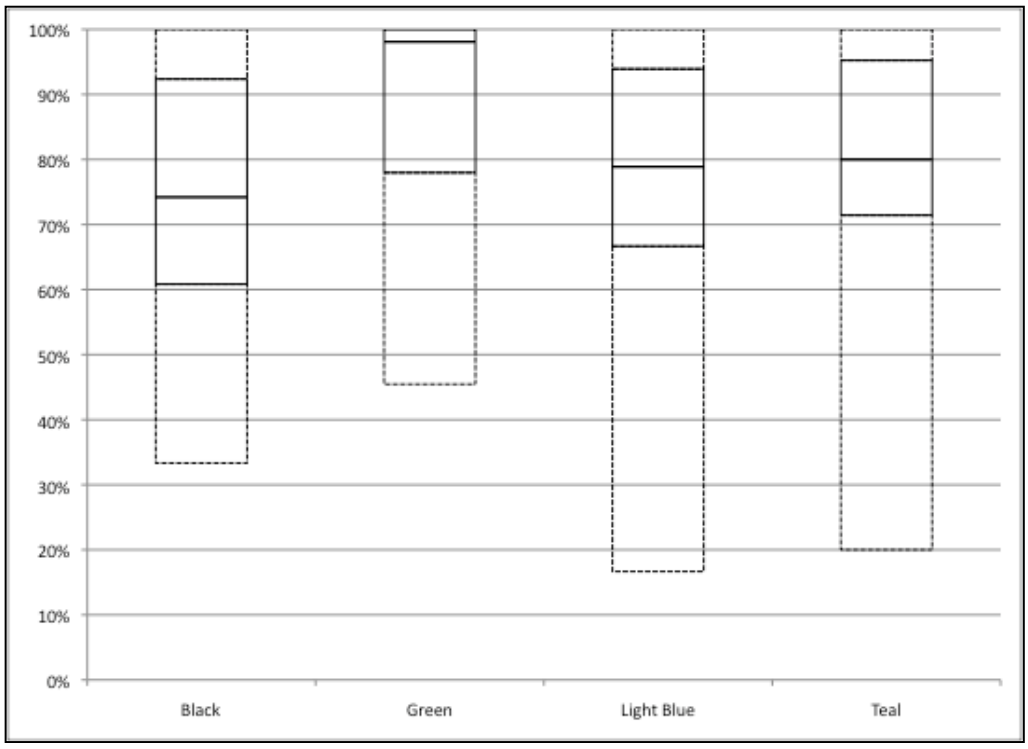


Figure 5.7 Boxplot comparison of all four study groups' arboreality. Y-axis indicates percentage of time spent arboreal.

5.7 Habitat Canopy Connectedness

Throughout their ranges, each group utilized habitats that were not covered by a continuous canopy. Specifically, from a lemur's perspective, in an open canopy, a lemur would not be able to travel continuously arboreally. Overall, the four study groups spent the vast majority of their time in closed canopy areas (closed: 69.5%; open: 30.5%, Figure 5.8a, Table 5.8). Consistent with other results such as vertical height use and arboreality, Reserve Groups spent significantly more time in closed canopy areas. This result reflects habitat differences between these groups of lemurs and how anthropogenic habitat alterations affect the daily pattern of habitat use among groups (Figure 5.8b, Table 5.9, Figure 5.9). Among the study groups specifically, there were no significant differences among direct comparisons between Teal and Green and Black and Light Blue (Figure 5.8c). However, Green and Teal Groups spent

significantly more time in closed canopy areas than either Black or Light Blue (Table 5.9, 5.10, Figure 5.10).

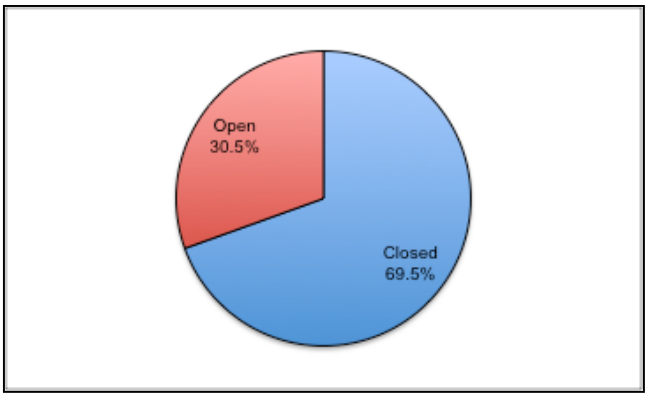


Figure 5.8a Overall closed and open canopy habitat usage for all study groups.

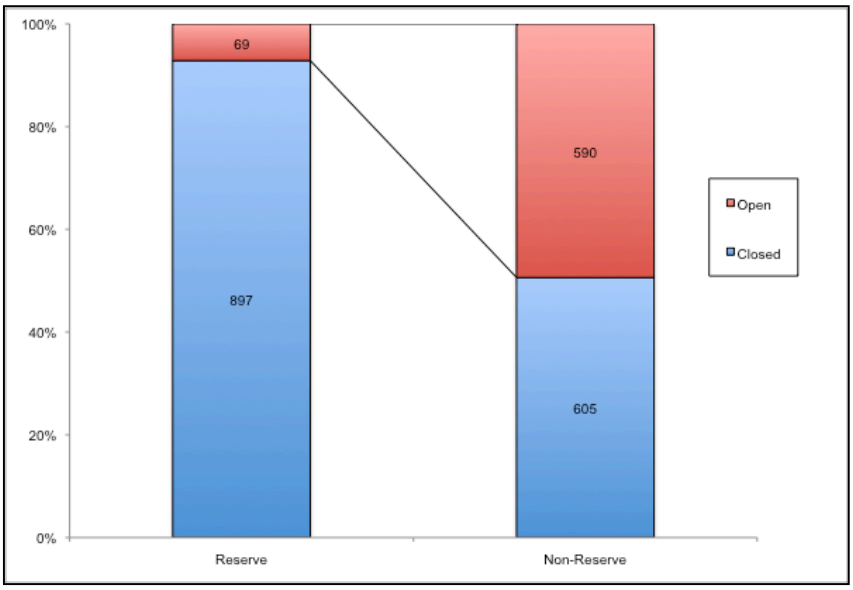


Figure 5.8b Percentage closed and open canopy habitat usage among Reserve and Non-Reserve Groups.

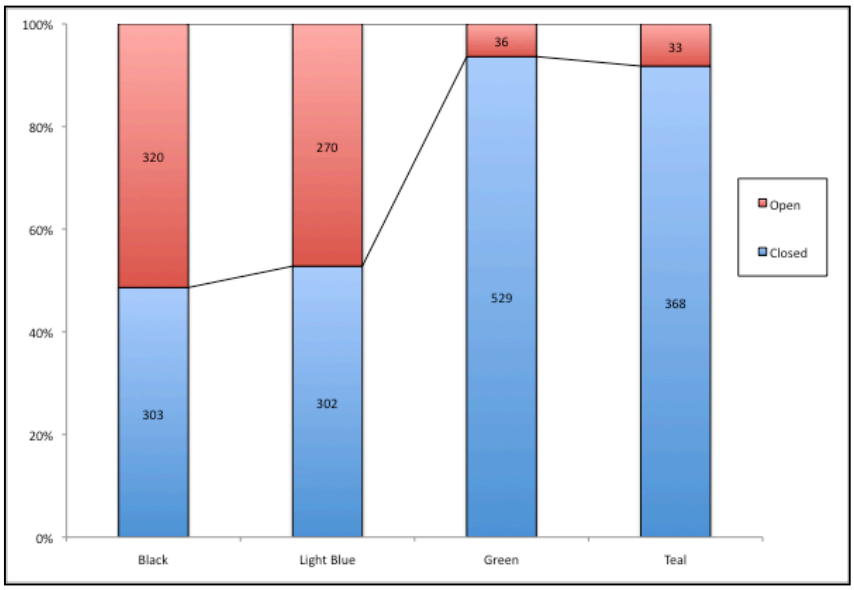


Figure 5.8c Closed and open canopy habitat usage among all four study groups.

Table 5.8 Closed and open canopy habitat usage among all four study groups.

	Closed	Open
Black	48.6%	51.4%
Light Blue	52.8%	47.2%
Green	93.6%	6.4%
Teal	91.8%	8.2%
Non-Reserve	50.6%	49.4%
Reserve	92.9%	7.1%
Total	69.5%	30.5%

Table 5.9 Average and median frequency of closed canopy habitat usage in each group.

Group	Average Daily Closed Canopy Habitat Frequency	Median Daily Closed Canopy Habitat Frequency
Black	7.07	6.00
Light Blue	7.27	6.50
Green	11.73	11.00
Teal	16.30	16.00

Table 5.10 Results from Kruskal-Wallis analysis of closed canopy usage among all four study groups and Reserve and Non-Reserve Groups.

Comparison of closed habitat usage among all four study groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	48.615	0.0001	Y	Y
Black vs. Light Blue	0.238	0.6255	N	N
Black vs. Teal	42.330	0.0001	Y	Y
Green vs. Light Blue	46.658	0.0001	Y	Y
Green vs. Teal	1.426	0.2325	N	N
Light Blue vs. Teal	38.975	0.0001	Y	Y
Comparison of closed habitat usage among Reserve vs. Non-Reserve Groups	**Value of K-W Test Statistic**	**P-Value**	**Reject H0 at 1% sig. level?**	**Reject H0 at 5% sig. level?**
Reserve vs. Non-Reserve	89.179	0.0001	Y	Y

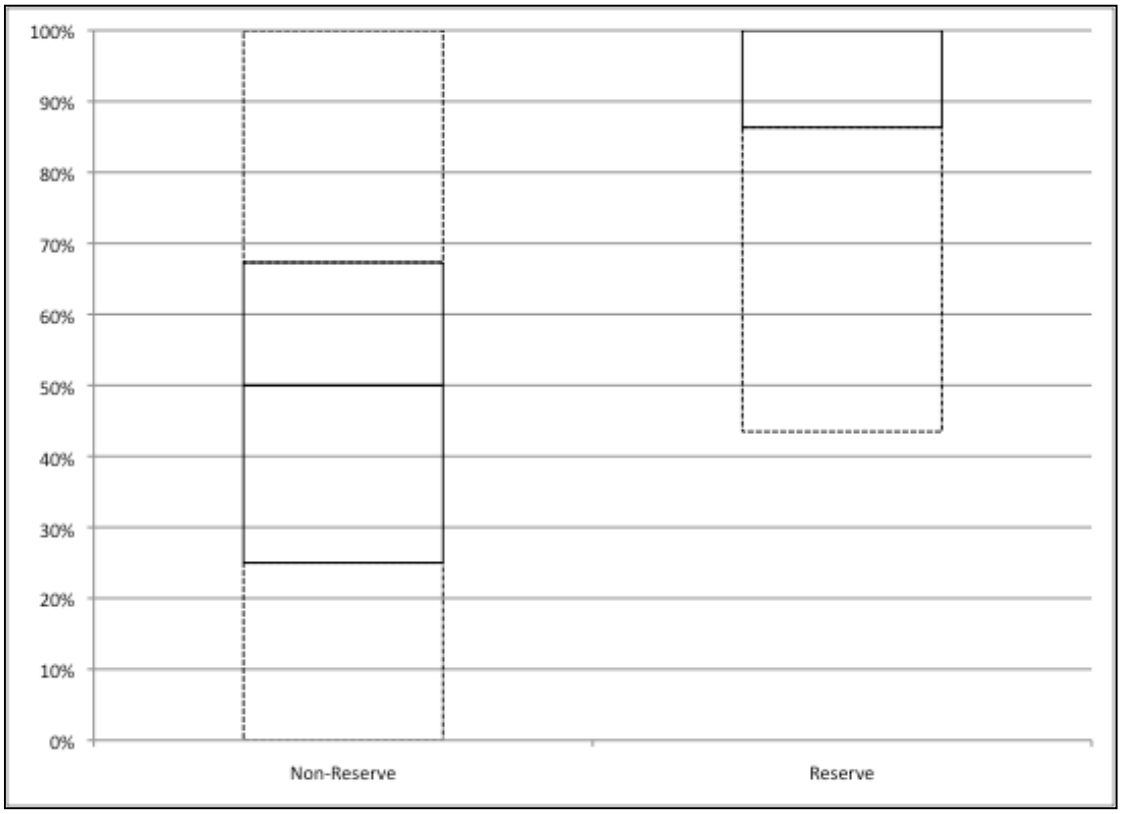


Figure 5.9 Boxplots of median percentages of Reserve vs. Non-Reserve closed canopy habitat usage.

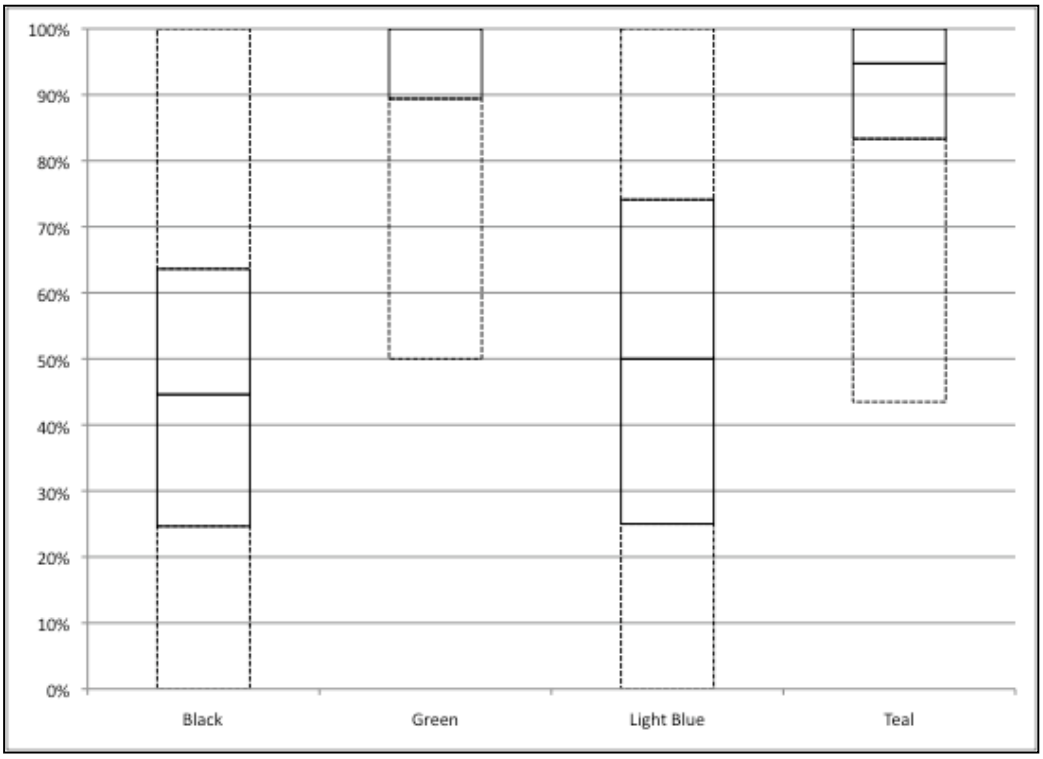


Figure 5.10 Boxplots of media percentages of closed canopy usage for all four study groups.

5.8 Terrestrial travel among study groups

To negotiate the habitat differences among groups and quantify the lemurs' strategies to move throughout their landscape, I noted how often the group traveled. Travel was described as coordinated walking or running in the same direction with all members participating. Overall, among the four study groups, they spent 7.8% of their time traveling compared to other activities such as resting and feeding (Figure 5.11a) (activity budgets will be examined extensively in the next chapter). For comparisons between the groups, I focused specifically on terrestrial travel because arboreal travel rarely occurred during the study period. Habitat did not directly predict the extent of terrestrial travel. Among the study groups, Light Blue Group traveled on the ground the most, then Black, Green and Teal (Figures 5.11b, 5.12). Comparisons among these groups

reveal that Light Blue traveled significantly more on the ground than either Green or Teal (Table 5.12), while Green, Teal and Black Groups were not significantly different from each other. Finally, both Black and Light Blue spent significantly more time traveling in open habitat than either Green or Teal (Table 5.13, 5.14).

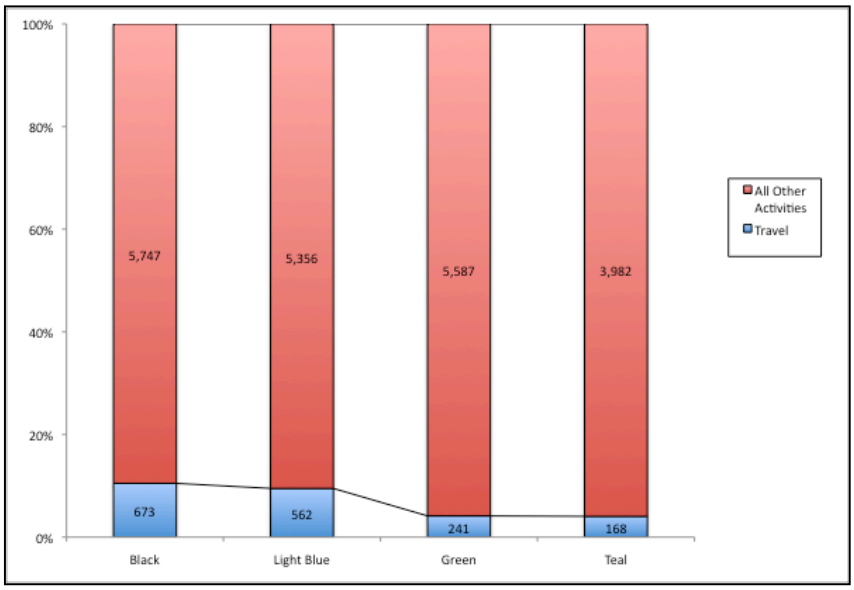


Figure 5.11a Overall time spent traveling among group behaviors.

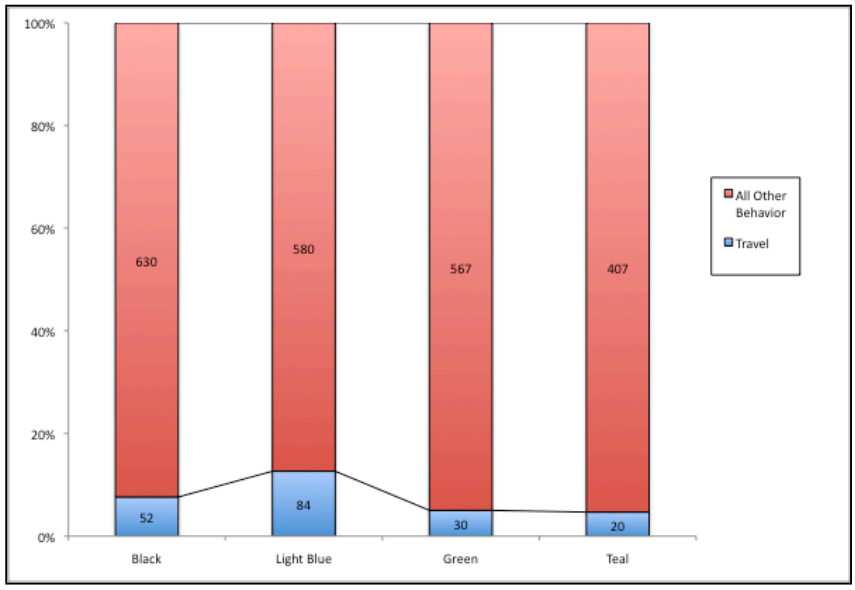


Figure 5.11b Comparison of percentage travel time on the ground among each of the study groups.

Table 5.11 Comparison of percentage travel time on the ground among each of the study groups.

	Terrestrial Travel	All Other Behavior
Black	7.6%	92.4%
Light Blue	12.7%	87.3%
Green	5.0%	95.0%
Teal	4.7%	95.3%
Non-Reserve	10.1%	89.9%
Reserve	4.9%	95.1%
Total	7.8%	92.2%

Table 5.12 Results from travel on the ground comparisons among all four study groups.

Comparison of terrestrial travel between study groups	Value of Kruskal Wallis Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	1.079	0.2988	N	N
Black vs. Light Blue	3.691	0.0547	N	N
Black vs. Teal	1.342	0.2468	N	N
Green vs. Light Blue	9.202	0.0024	Y	Y
Green vs. Teal	0.008	0.9303	N	N
Light Blue vs. Teal	8.396	0.0038	Y	Y

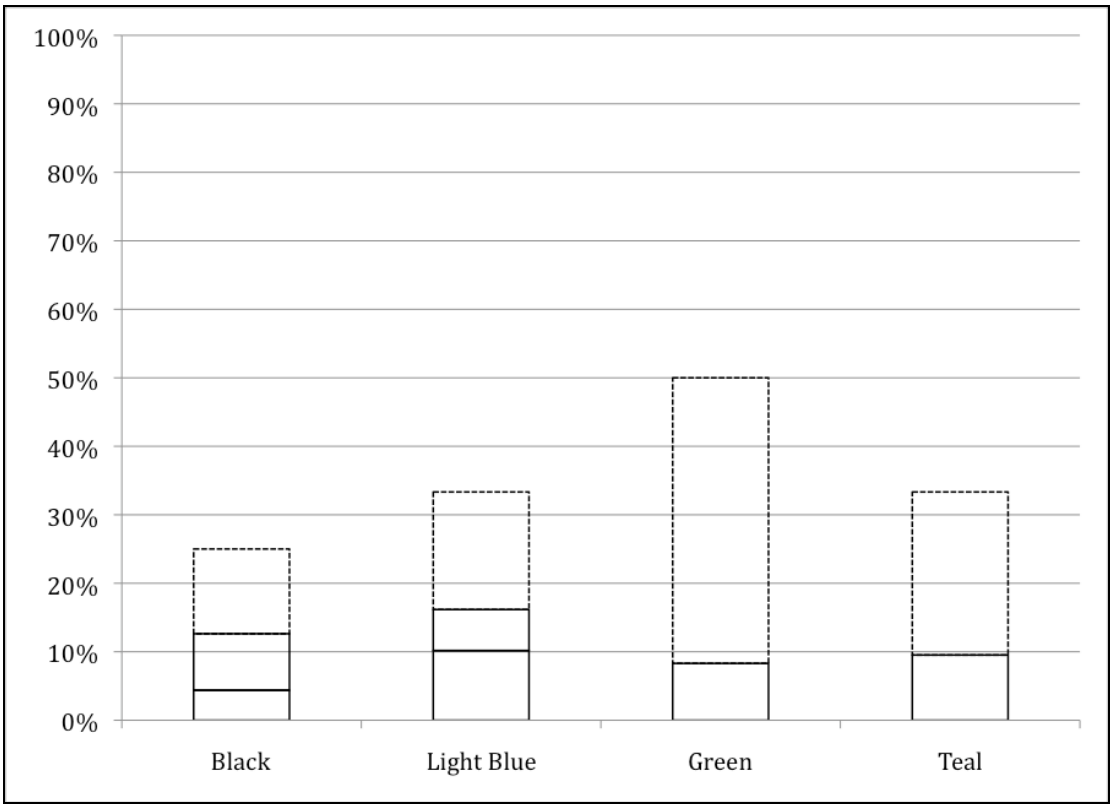


Figure 5.12 Boxplot describing all four groups percentage of time traveling on the ground.

Table 5.13 Frequency of travel in open habitats (no canopy overhead) for each group.

Group	Open Canopy Habitat and Traveling Frequency
Black	19
Light Blue	45
Green	6
Teal	2

Table 5.14 Results from travel in open and closed canopy habitat comparisons among all four study groups and Reserve versus Non-Reserve pooled data.

Comparison of travel in open and closed habitats between all four study groups	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	1.079	0.0213	Y	Y
Black vs. Light Blue	3.691	0.7325	N	N
Black vs. Teal	1.342	0.0312	Y	Y
Green vs. Light Blue	1.126	0.0024	Y	Y
Green vs. Teal	9.202	0.9303	N	N
Light Blue vs. Teal	1.032	0.0038	Y	Y
Comparison of travel in open and closed habitats between Reserve and Non-Reserve Groups	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Daily mix of closed/open	89.179	0.0001	Y	Y

5.9 Anthropogenic habitat disturbance ratings in habitat usage among groups

As might be expected from the description of Reserve versus Non-Reserve habitats at BMSR, there are significant differences between habitat classifications among the groups (Figures 5.13a, b, 5.14, Table 5.16, 5.17). Immediately after an individual follow, I classified the current habitat that the lemurs were using into a continuum of forest disturbance running from 1=least disturbed to 6=most disturbed (fragmented, anthropogenically altered habitats; Table 5.15, 5.16, 5.17). Degradation variables included evidence of tree cutting, presence of livestock feces, grazing, roads, crops and severe deforestation. When more variables are present, the disturbance score is higher. As expected, results indicate that Black and Light Blue Groups spend a significantly higher amount of their time in more disturbed habitats. Black Group's median habitat type is 3, with three degradation/disturbance variables present, and Light Blue Group's is 4, with four degradation/disturbance variables present (Figure 5.14). Comparisons

between all four study groups indicate that Light Blue Group's habitat disturbance level is significantly higher than all groups, Black Group's habitat disturbance is higher than each of the Reserve Groups, and Green and Teal Groups are similar in habitat disturbance level (Figure 5.14, Table 5.16, 5.17). As such, Non-Reserve Groups habitat disturbance level is also significantly higher than the levels of Reserve Groups (Table 5.16, 5.17, Figure 5.15).

Table 5.15 Habitat Classification variables. Degradation variables include evidence of tree cutting, presence of livestock feces, grazing, roads, crops, severe deforestation.

Habitat Classification	Habitat Variables Present
0	0/5 variables present
1	1/5 degradation variables present
2	2/5 degradation variables present
3	3/5 degradation variables present
4	4/5 degradation variables present
5	5/6 degradation variables present
6	All variables present

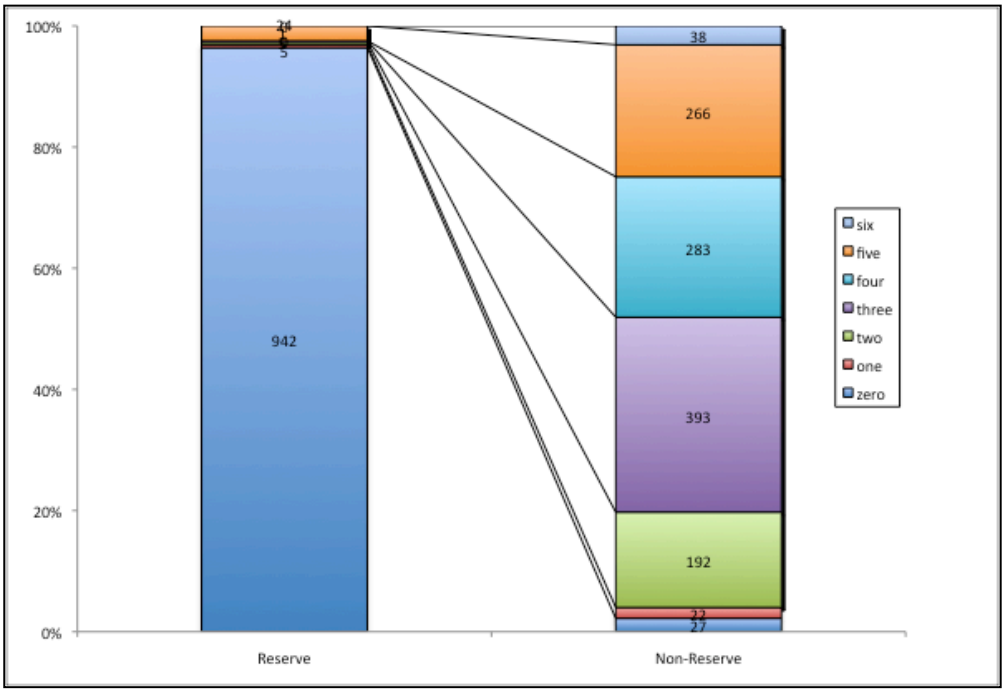


Figure 5.13a Reserve and Non-Reserve frequency of habitat usage according to level of disturbance.

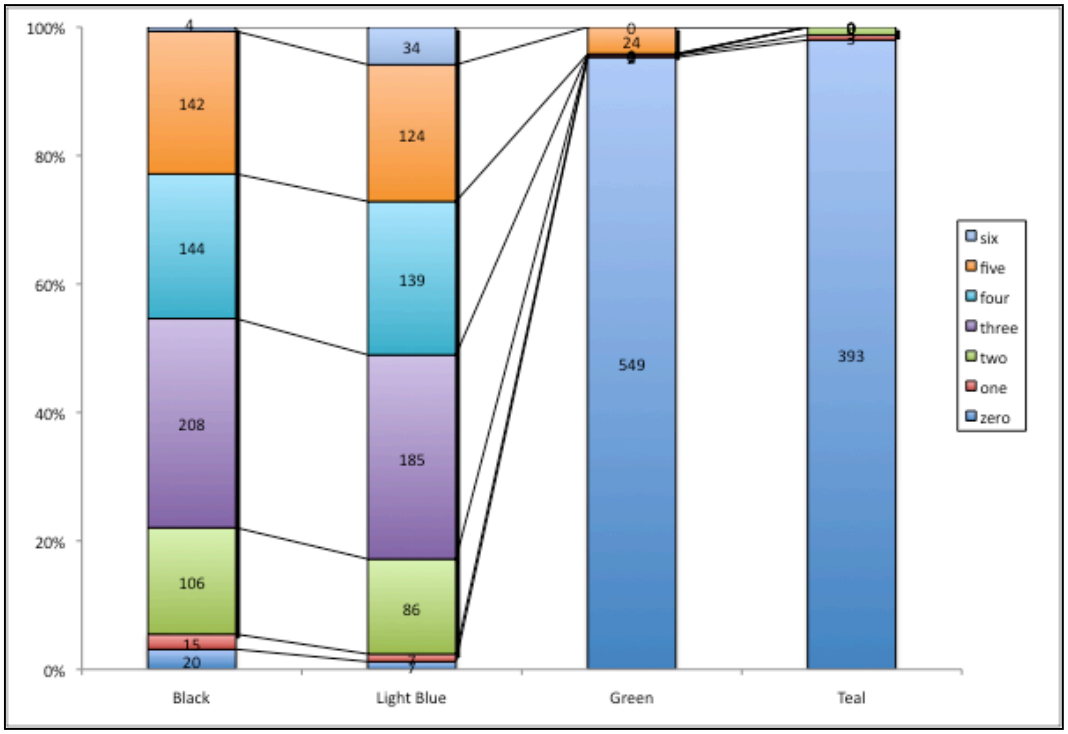


Figure 5.13b All groups' frequency of habitat usage according to level of disturbance.

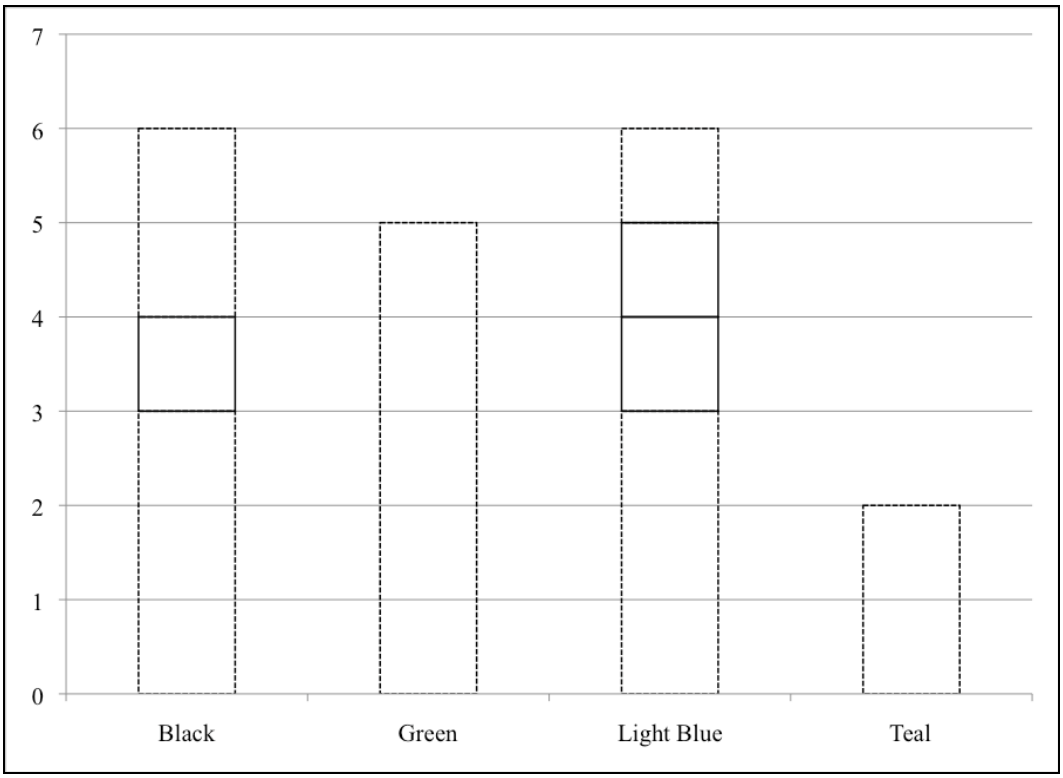


Figure 5.14 Boxplot comparison of all four groups' median habitat disturbance levels. Green and Teal appear to have no median because the disturbance variables were relatively Non-existant.

Table 5.16 Frequency of each group's habitat disturbance level and median disturbance level.

	Zero	One	Two	Three	Four	Five	Six	Median
Black	20	15	106	208	144	142	4	3
Light Blue	7	7	86	185	139	124	34	4
Green	549	2	0	1	0	24	0	0
Teal	393	3	5	0	0	0	0	0
Non-Reserve	27	22	192	393	283	266	38	3
Reserve	942	5	5	1	0	24	0	0
Total	969	27	197	394	283	290	38	2

Table 5.17 Results from Kruskal-Wallis test of comparisons between all four group's habitat disturbance levels and of Reserve versus Non-Reserve Groups' habitat disturbance levels.

Comparison of habitat disturbance level between all four study groups	**Value of Kruskall Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	727.350	0.0001	Y	Y
Black vs. Light Blue	7.920	0.0049	Y	Y
Black vs. Teal	688.007	0.0001	Y	Y
Green vs. Light Blue	730.737	0.0001	Y	Y
Green vs. Teal	0.546	0.4601	N	N
Light Blue vs. Teal	691.046	0.0001	Y	Y
Comparison of habitat disturbance level between Reserve and Non-Reserve Groups' pooled data	**Value of Kruskall Wallis Test Statistic**	**P-Value**	**Reject H0 at 1% sig. level?**	**Reject H0 at 5% sig. level?**
Non-Reserve vs. Reserve	1420.204	0.0001	Y	Y

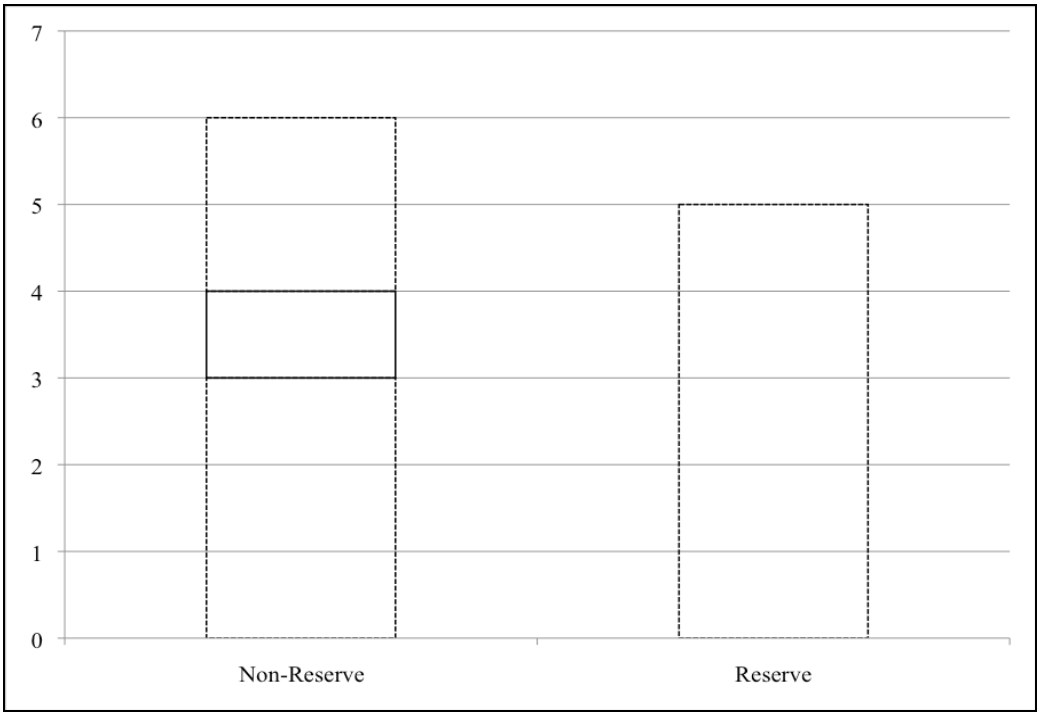


Figure 5.15 Boxplot comparison of Reserve vs. Non-Reserve median habitat disturbance levels. Here the Reserve medians are close to zero because the disturbance levels are very low.

5.10 Group Spread

At each group data collection (after each 10 min. individual focal) I collected data on group spread. These group spread parameters included sitting close (sitting in contact), close (2-4 m), medium (4-6 m), far (6-12 m), very far (>12 m). Considering the travel, and social behaviors reviewed thus far, one would expect some differences between groups' cohesiveness, and between pooled data of Reserve and Non-Reserve Groups. For statistical analysis, I assigned numbers to each qualitative assessment: 1 = very close, 2 = close, 3 = medium, 4 = far, and 5 = very far. Overall, groups spend the majority of their time in close proximity (2-4 m apart; Figure 5.16a). Results from comparing Reserve and Non-Reserve Groups were highly significant (p=0.0001), with Non-Reserve Groups spending more time in less cohesive group member arrangements (Table 5.18, Figure 5.16b, 5.17). When compared by group, Green was the most cohesive in terms of group spread, then Teal, Black, and Light Blue (Figure 5.16b, 5.17; Table 5.18, 5.19). Black and Light Blue Groups were significantly more spread out than both Green and Teal (p=0.0001), and Green was significantly and consistently less spread out than Teal Group (Figure 5.16c, 5.18). These results were corrected for group size.

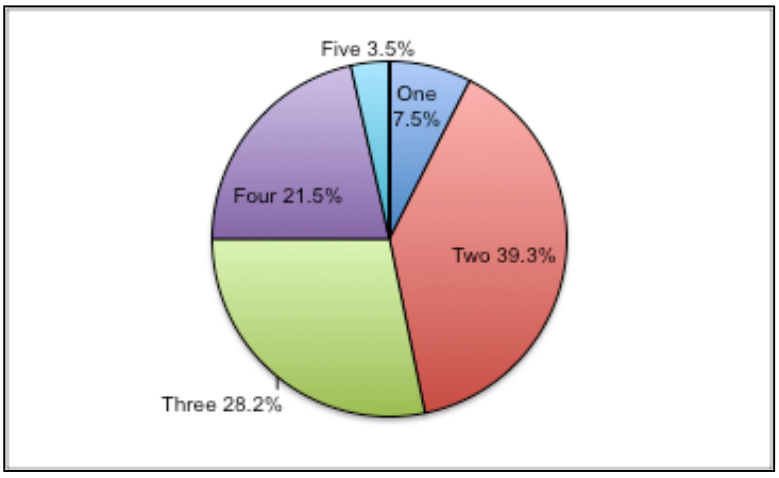


Figure 5.16a Overall percentage group spread results for all four study groups.

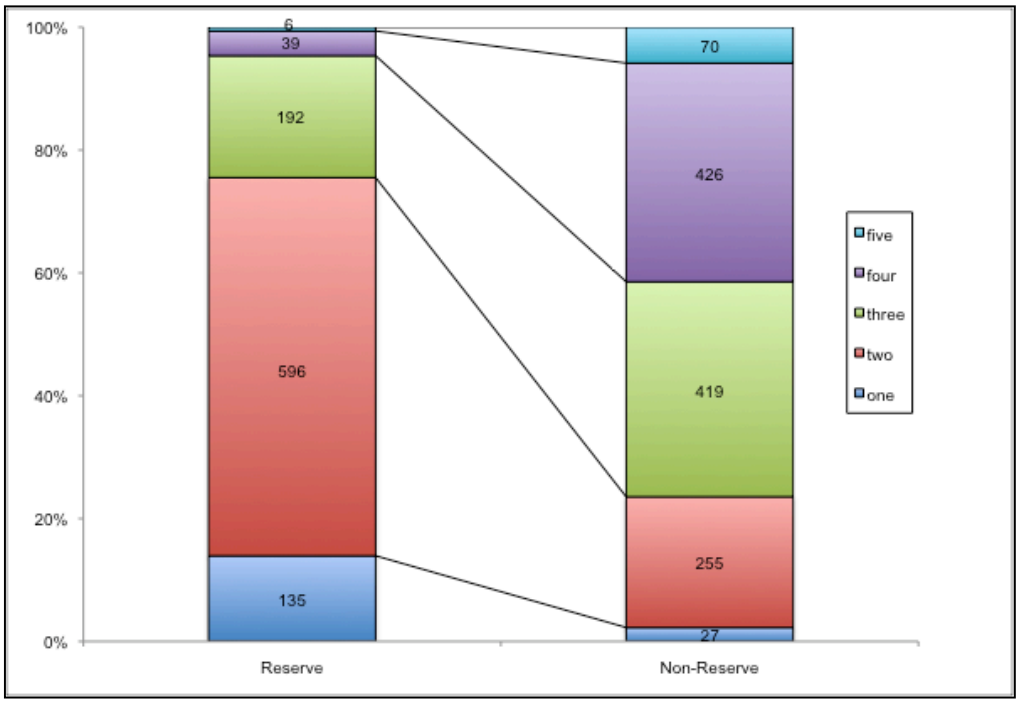


Figure 5.16b Frequency Reserve vs. Non-Reserve Group spread results.

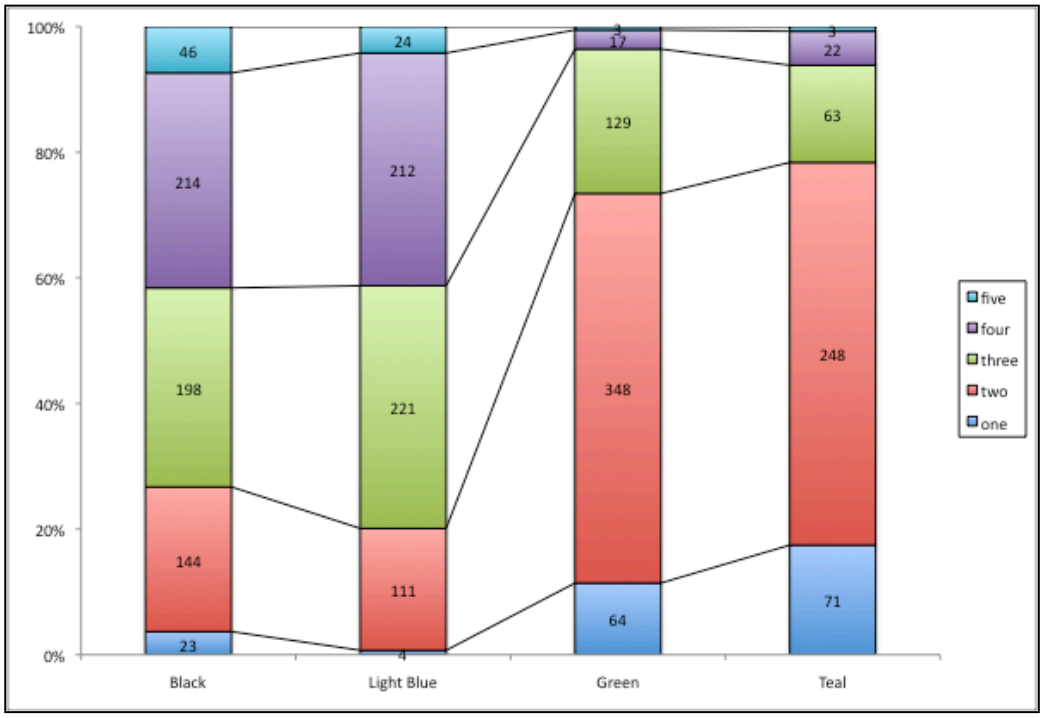


Figure 5.16c Frequency of group spread results for all four study groups.

Table 5.18 Percentage of time each group spent in each group spread categories.

	One	Two	Three	Four	Five
Black	3.7%	23.0%	31.7%	34.2%	7.4%
Light Blue	0.7%	19.4%	38.6%	37.1%	4.2%
Green	11.4%	62.0%	23.0%	3.0%	0.5%
Teal	17.4%	60.9%	15.5%	5.4%	0.7%
Non-Reserve	2.3%	21.3%	35.0%	35.6%	5.8%
Reserve	13.9%	61.6%	19.8%	4.0%	0.6%
Total	7.5%	39.3%	28.2%	21.5%	3.5%

Table 5.19 Kruskal-Wallis results for comparing the frequency (number of times each group was observed in each spread category) of group spread results between all four study groups and Reserve versus Non-Reserve Groups.

Comparison of group spread among all four study groups	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	273.376	0.0001	Y	Y
Black vs. Light Blue	0.740	0.3897	N	N
Black vs. Teal	249.150	0.0001	Y	Y
Green vs. Light Blue	338.589	0.0001	Y	Y
Green vs. Teal	4.472	0.0345	N	Y
Light Blue vs. Teal	302.952	0.0001	Y	Y
Comparison among Reserve vs. Non-Reserve study groups	**Value of Kruskal Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve vs. Non-Reserve	580.568	0.0001	Y	Y

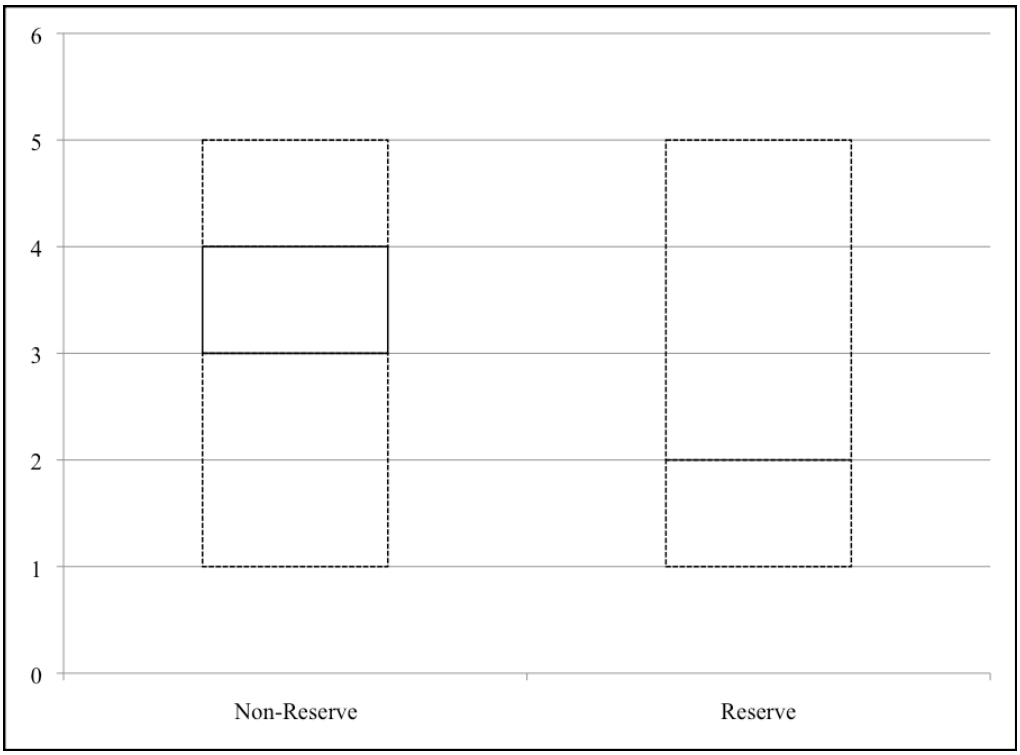


Figure 5.17 Boxplot comparing Reserve versus Non-Reserve Group spread results.

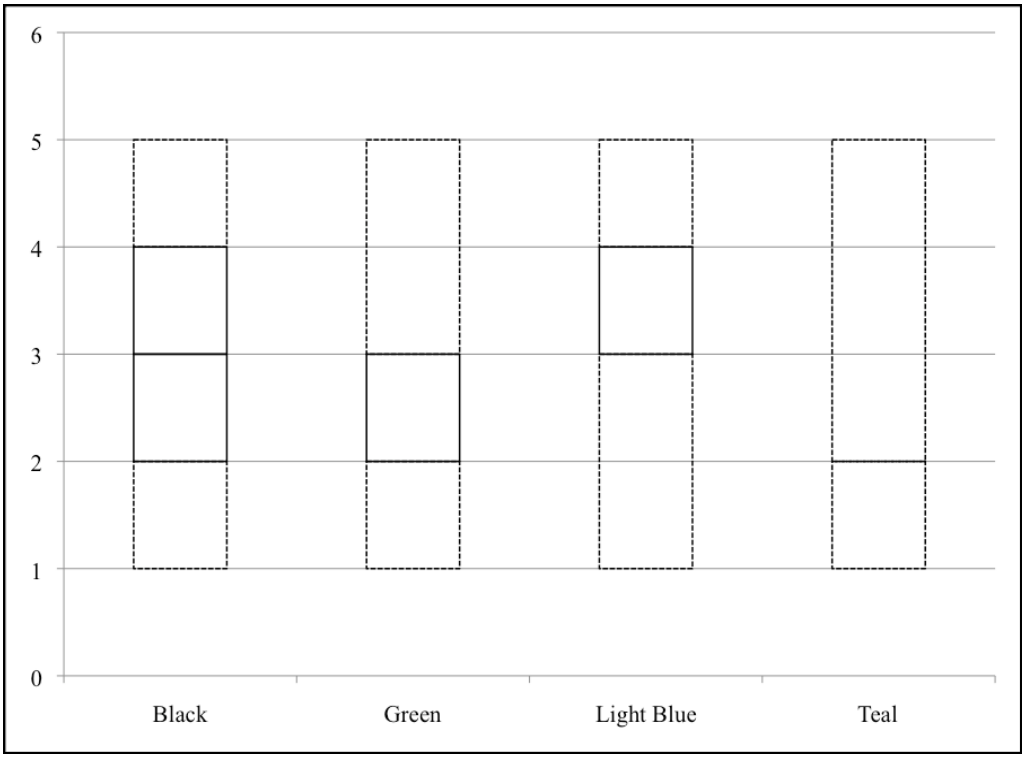


Figure 5.18 Boxplot compaing all four study groups' group spread results.

5.11 Discussion

In previous chapters, I have presented evidence that anthropogenic habitat disturbance has had effects on the structure and composition of the landscape surrounding the BMSR. Additionally, there are differences in feeding strategies, both diversity of diet and feeding and foraging, among groups. This chapter investigates the effects of these changes on ring-tailed lemurs' use of space in and around BMSR. Since spatial distribution of food resources is perhaps the most primary factor in an organism's use of space, I expected to see ring-tailed lemurs in anthropogenically altered areas to show differences in ranging patterns, habitat use, and some spatially oriented behaviors such as traveling and group spread during the active period.

Home range size is reduced in anthropogenically altered habitats: Black and Light Blue Groups are 20% to 50% smaller than Green and Teal home ranges. This is consistent with other primate groups in altered, fragmented, and disturbed areas (Estrada and Coates-Estrada 1996, Estrada et al. 1999, 2002, Irwin 2006, MeNon and Poirier 1996, Onderdonk and Chapman 2000). Accepting this as a rule across species may underestimate the complexity of variables at work. For instance, this probably reflects interspecific dietary flexibility. It also reflects a variable present among primates that are found in anthropogenically altered habitats. Namely, species that are able to tolerate and persist in altered landscapes (at least in the short term) may also have a set of characteristics that allow them to do so. It is possible that a subset of primate species is able to find a higher density of suitable resources, hence, they are able to utilize smaller home ranges and higher densities. Those species that are not successful in altered and fragmented habitats will most likely be absent from altered landscapes and a comparison may not be possible. It will prove enlightening to learn about more species and their strategies for inhabiting

altered habitats – this will prove useful for identifying which particular charactistics allow species to persist in challenging and anthropogencially dynamic areas. A few projects have illustrated that perhaps folivorous taxa may be predisposed to survive in altered habitats (Ganzhorn 1995, Irwin 2006) and predominantly frugivorous taxa to be less tolerant of constrained habitats (Johns and Skorupa 1987). As has been indicated in this dissertation, variability appears to be the norm, rather than the exception. For example, lion-tailed macaques (*Macaca silenus*) are a signficant exception. Populations of this species survive in India with reduced home ranges while being mainly frugivorous. Despite fruit being the dominant dietary component for lion-tailed macaques in undisturbed areas, groups inhabiting more anthropogenically altered habitats consume more flowers, thus illustrating primate flexibility (Umapathy and Kumar 2000b). Simplified dietary categories, such as frugivorous or folivorous, are useful to predicting a rough tolerance of altered habitats, but it is clear that subtle nuances in diet, flexibility, and the types and distributions of preferred high quality food resources, also must be considered to fully understand primate persistence and population success in challenging landscapes.

Daily path length (DPL) was even a more drastic change than home range size for ring-tailed lemur groups in habitats outside the protected Reserve. This result was surprising given the general lack of concordance of home range and day range among many well-studied primate species. For example, Bicca-Marques (2003) found a lack of significance between DPL and fragment size in a metaanalysis of *Alouatta* species in disturbed landscapes in Central and South America. Even among other Malagasy primates, such as sifakas, daily ranges are remarkably similar despite habitat and climate differences in the northern, western, and southern parts of Madagascar (Irwin 2006, Powzyk 1997, Richard 1978, Wright 1987). In contrast to these

studies, ring-tailed lemurs in this study appear to lengthen DPL in response to the multiple variables associated with smaller home ranges. As discussed in the previous chapter and this chapter, Non-Reserve Groups forage signficantly more, and maintain a larger group spread. Therefore, it is possible that changes in food resource distribution and social factors are the motivating variables for groups in altered habitats to maintain longer travel distances.

In terms of DPL and feeding strategies, Non-Reserve Groups travel more and focus on a more diverse array of resources than Reserve Groups. It is possible that Reserve Groups are able to access larger food patches that allows them to travel less and feed at fewer sites. Non-Reserve Groups may therefore need to maintain longer DPLs because of the increased number of patches they must find in a given day. This is consistent with differences in home range reported for two nocturnal lemurs of similar body size (Warren and Crompton 1997): *Avahi occidentalis* (home range: 1.64 ha) is a more selective feeder, with a more patchy resource distribution, whereas *Lepilemur edwardsi* (1.09 ha) is less selective, with a more even resource distribution. It is also consistent with a detailed study of diademed sifakas in eastern Madagascar where groups in fragments relied heavily on mistletoes (which exist as small, dispersed patches) and maintained longer DPLs than groups in continuous forests nearby (Irwin 2007). Furthermore, Black and Light Blue Groups both have a higher degree of edge habitat relative to interior forest space. Their longer DPLs fit well with the pattern of disturbance tolerance that Ganzhorn (1995) discussed. Moderately disturbed edges tend to be utilized extensively, even though core areas are in the intereior of their ranges, because: 1) light exposure at edges tends to increase leaf quality (higher protein: fiber ratio), and 2) higher plant diversity in habitat interiors may "dilute" the density and efficiency of preferred resources (Ganzhorn 1995, Ganzhorn et al. 1997). With this in mind, it is possible that Non-Reserve Groups were traveling more extensively to access

the edge habitats, and their resources, on all sides of their ranges. This is also reflected in both the canopy connectedness and habitat disturbance rating data: Non-Reserve Groups utilize open canopy areas and habitats with higher degrees of disturbance to a greater extent than do Reserve Groups. Edge habitats, and habitats towards the exterior of altered areas, are more open which, in turn, allows more sunlight to reach the trees that remain. Edge habitats surrounding BMSR tended to support highly preferred resources such as kily (*Tamarindus indica*), tratraborondreo (*Grewia leucophylla*), filo filo (*Azima tetracantha*), tsikidratse (*Bridelia* sp.), and kotipoke (*Grewia grevei*). This was measured qualitatively with photographs of all edge habitats during the study period.

Additionally, DPL can sometimes be explained by increased territorial defense; primates may choose to range more than is necessary to maintain adequate resource acquisition and to patrol and mark territorial boundaries (Irwin 2006, 2007, Warren and Crompton 1997). At BMSR, the anthropogenically altered nature of the landscape actually reduces the number of potential encounters (see Chapter 7), but territorial boundaries may be historically and adaptively retained even after neighboring groups have disappeared.

Non-Reserve Groups spent more time in lower forest levels of the trees and more time traveling terrestrially, especially in areas of open canopy. These results suggest that Non-Reserve lemurs may be more susceptible to ground-dwelling predators, less likely to be feeding on high quality fruits in the trees, and exposing themselves to other species' feces (especially domestic grazers), and raptors. Additionally, Non-Reserve Groups were also more likely to be less cohesive in all activities (i.e. larger group spread). Larger group spread in these lemur groups may be a consequence of less dense food patches, lower quality resources and may have

negative consequences on social dynamics, social relationships, and predator defence via vigilance.

Ring-tailed lemurs appear to compensate for anthropogenically altered habitats by traveling for a higher percentage of time than groups inside BMSR, longer daily path lengths, and larger group spread to access a higher diversity of resources. Additionally, there is little evidence that predation pressure is limiting populations inside BMSR (see Chapter 8). In fact, with higher incidences of predation in anthropogenically altered habitats, lower reproductive success, higher rates of traveling, more time spent foraging, and more widely scattered food patches ring-tailed lemurs in Non-Reserve habitats may be more stressed energetically and this might prove to be too costly in the long-term for population persistence.

Nonetheless, ring-tailed lemurs in anthropogenically altered habitats appear to have the capacity and flexibility necessary to survive in these landscapes, at least in the short term. Continuing studies at BMSR will elucidate the long-term viability of populations in altered habitats specifically addressing consequences in social behavior arising from ecological shifts that might threaten the stability of social groups (such as prolonged decrease in group cohesiveness); demographic constraints such as altered fertility, fecundity, survival rates, injury and recovery rates, constrained dispersal across habitats; and physiological effects of altered diets such as well as effects on health and body condition, and altered prevalence of disease and parasites. While this study has documented short-term survival of these populations outside the protected area and their strategies for mitigating an altered resource landscape, these variables, in any combination or amount, may cause an overall negative pressure on population growth rate in the anthropogenically altered habitats, thus negating any short-term advantage of increased resource base due to edge effects. Ring-tailed lemur groups outside the Reserve would then

represent sink populations, or temporary populations that are on a trajectory towards local extinction. There are only a handful of forests in Madagascar that unfortunately do not fall into these categories of altered, disturbed, and fragmented (Green and Sussman 1990, Irwin et al. 2005). It is therefore prudent to understand the process and fate of populations in these habitats, and this understanding will increase the effectiveness of conservation and management plans to find and protect the best habitats that have the combination of resources most needed for populations to survive and persist.

CHAPTER 6

EFFECTS OF ANTHROPOGENIC HABITAT DISTURBANCE ON *LEMUR CATTA*: ACTIVITY PATTERNS

6.1 Introduction

6.1.1 Anthropogenic habitat disturbance and activity alterations

Anthropogenic habitat disturbance may affect species' activity budgets via local changes in abiotic and biotic variablies. Abiotically, temperature fluctuations may affect metabolic rates during the day (Irwin 2006). For example, forest fragments at Tsinjoarivo in eastern Madagascar had higher maxima and lower minima temperatures. Researchers there noted that sifaka residing in fragments incurred longer daily activity periods, but rested more than sifaka in neighboring continuous forests (Irwin 2006, 2007). Biotically, anthropogenic habitat disturbance can affect the diets of primates in disturbed areas. These dietary changes may alter ranging patterns; energy available for activities due to the quality of diet; and longer term effects on a population such as nutrition, health, and demography (Irwin 2008). As more research has been conducted in anthropogenically disturbed habitats, activity budgets have been shown to vary with different degrees of habitat disturbance, yet patterns are still unclear (Altman and Muruthi 1988, Isbell and Young 1993, Iwamoto and Dunbar 1983, Johns 1986, Oates 1977, Singh and Venanthe 1990, Watts 1988). In addition to short term activity budget changes, a few studies have also shown demographic changes in group size that in turn alter group activity patterns (Dunbar 1992, Teichroeb et al. 2003, van Schaik et al. 1983).

While limited, there are a several studies that have specifically examined the effects of habitat disturbance on activity patterns of primate species. In India, lion-tailed macaques residing in fragmented forests (*Macaca silenus*) were recorded spending more time traveling than either feeding or resting than groups in neighboring continuous forests (MeNon and Poirier

1996, Umapathy and Kumar 2000b). The researchers concluded that groups in fragmented forests require more traveling time to compensate for dispersed resources. However, they also noted that group sizes vary in fragment groups, thus enabling higher feeding rates at feeding sites. From these data, it is difficult to discern which variable is causative in these examples: altered group size due to demographic changes or habitat variables. Small, but significant changes were found when comparing sifaka groups (*Propithecus diadema*) in eastern Madagascar. Specifically, groups in fragments spent more of their active time feeding and arrived later at sleeping sites (Irwin 2006, 2007). While these alterations do not seem to affect these groups in the short term, over time it is unknown whether small changes in diet, activity, and group size will detrimentally change population success in disturbed habitats.

Research examining activity patterns in howlers and black-and-white colobus indicated no changes in activity budgets when comparing groups in disturbed versus continuous forests. For instance, howler monkeys in a small forest fragment (3.6 ha) had an almost identical activity budget to groups in neighboring continuous forests (Estrada et al. 1999). This is particularly interesting because howlers in these small fragments had dramatically different diets and group densities compared to groups residing in unaltered forests. During a short study (3 months) on black-and-white colobus, the same pattern emerged. There were no differences in activity budgets for the colobus, yet significant differences in other ecological variables: diet, group size, and home range (Onderdonk and Chapman 2000). In these examples it appears that activity budget changes occur more often in frugivores and smaller bodied folivores (*Propithecus diadema*), than larger bodied folivores.

6.1.3 Activity Patterns of *Lemur catta*

Malagasy primates across the island exhibit strong seasonal patterns in their activity (Wright 1999, Deghan 2003, Ganzhorn et al. 2000). Comprehensive activity budget data have been reported for *Lemur catta* at Berenty (Jolly 1966, Rasamimanana et al. 2006) and BMSR (Loudon 2009, Sauther 1992). Activity budget reports for *L. catta* at Berenty show that individuals spend approximately the same amount of time during the day being active (comprising feeding, moving, traveling, grooming, and sunbathing) as they do resting (Rasamimanana et al. 2006) (Figure 6.1).

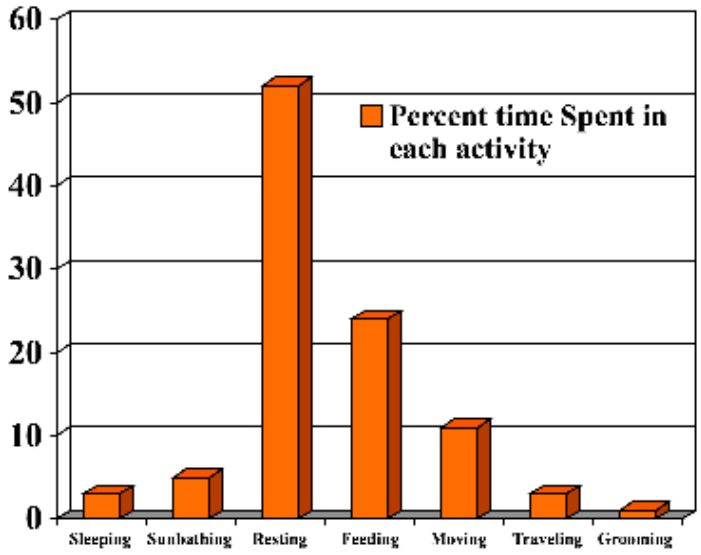


Figure 6.1 Activity budget for male and female *Lemur catta* at Berenty. Data from Rasamimanana et al. 2006.

Most available activity budget data from BMSR has been tied to parturition, mating season, lactation, and gender differences in great detail (Gould 1994, Loudon 2009, Sauther 1992). These studies have shown that because of the seasonality of resources and the highly seasonal mating pattern, activity patterns tend to vary throughout the year (Sauther 1992). Groups tend to spend more time resting during the dry season than in the wet season (Loudon

2008, Sauther 1992). Certainly, during the dry season, morning temperatures can dip below 40° Farenheit, and ring-tailed lemurs tend to rest until temperatures rise during the late morning (Loudon 2008, Sauther 1992, Whitelaw pers. obs). Overall, peaks in resting tend to correlate with a decrease in time spent feeding, and vice versa; when feeding increased, individuals spent less time resting (Gould 2006). Similarly, females also reduced allogrooming when feeding increased. Generally, feeding time tends to be similar for all classes of individuals (Sauther 1992). Females, however tend to move, travel, and groom more than males (Rasamimanana et al. 2006). *L. catta* spends a similar amount of time resting as other lemurs. In terms of social behavior, at BMSR, social behavior has been documented as 2.6% of the daily budget (Sussman and Garber 2004). Within this proportion, 2.5% was classified as affiliative, and 0.5% as agonistic.

6.1.4 Objectives

Chapter 6 will examine the effects of anthropogenic habitat disturbance on the activity patterns of *L. catta* at Beza Mahafaly Special Reserve. Specifically, I will address whether habitat disturbance affects time spent active as well as the amount of time spent among activities, such as feeding, grooming, traveling, and resting. I will also ask whether activities such as feeding, traveling, and resting vary with seasonal changes and whether there is a correlation between activity patterns and dietary composition for the different habitats.

Answers to these questions will lend clarity to how activity patterns are affected by environmental changes in their habitats. Consequently, wildlife conservationists will be able to make data-driven decisions regarding priorities of conservation management and protection. Additionally, this work will add important information towards understanding how some primate species persist and successfully adapt to habitat disturbance, while some species are not tolerant

of such changes. As primatologists, most of our resources in the literature pertain to studies focusing on populations in protected and undisturbed areas, although this is changing as populations become increasingly endangered, and populations in pristine areas are increasingly difficult to find. As a result, relatively little is known about primate behavioral ecology in anthropogenically disturbed and altered habitats. This study contributes to the growing body of knowledge that will bridge this gap in the literature and produce valid data for sound conservation management decisions of endangered species. Finally, using comparative methods to examine groups within undisturbed areas and altered habitats also provides interesting and important information for components of behavioral ecological theory.

6.2 Methods and Analysis

6.2.1 Data Collection

I collected behavioral data on the four study groups detailed above between October 2005 and June 2006. These months captured both the wet and dry seasons in the BMSR region. In general, I cycled through the Reserve and Non-Reserve Groups examining each group for two days in the following repeating order: Green, Teal, Black, Light Blue. Groups proved difficult to locate, particularly those outside the Reserve and this method ensured that I could locate them early on the second day having noted their sleeping site the day before. Observations were made during day-long group follows and rotated through individual group members so as to equalize sample size among individual lemurs. Habituation and distance estimation were established during September 2005.

All behavioral data were collected on a hand-held, Palm LifeDrive © in Excel. I used the BMSR solar panels to recharge the device the LifeDrive © each afternoon, except when rainy

season monsoons prevented the solar panels from being charged. I stored data on rewritable compact discs each week.

In the mornings, as often as possible, I located groups in their sleeping trees or as soon as they began moving. I used 10 - minute focal samples with a 1-minute interval to record behavior (Altmann 1974). For each minute I collected the following information: focal individual behavior, location and species of tree involved if individual was arboreal, plant part if feeding, arboreal height (0 if terrestrial), nearest neighbor distance, nearest neighbor location in tree, nearest neighbor height, nearest neighbor behavior. For each 10 minute sample, I also recorded all occurrences of aggression, inter-troop encounters, GPS location if any movement over 20 meters had occurred, general group behavior, group spread, group location in terms of terrestriality or arboreality, and canopy connectedness, group spread (sit close, sitting in contact; close, 2-4 m; medium, 4-6 m; far, 6-12 m; or very far, >12 m), and if the group was traveling. Additionally, I classified the habitat that lemurs were using in a ranking system to quantify the degree of disturbance. Based on the number of degradation variables present, I gave the habitat (area within 50 m) a number 1-5 depending on the number of the following variables present: evidence of tree cutting, presence of livestock feces, grazing, roads, crops. These group variables were recorded according to the majority of individuals' behavior, location, etc. These data, using the number of intervals of the particular behavior, location, and habitat classification, allows me to calculate group behaviors and compare between study groups.

6.2.2 Data Analysis

Total sample size on which the analyses are based is almost 300 group follow days which encompass almost 800 hours of contact time. For all analyses involving overall daily activity

patterns, the full dataset was used. Any grossly incomplete days were excluded so as not to bias the results towards activities that might tend to occur during the period observed.

To quantify activity budgets, these analyses are expressed as proportions of observed active records. These records occur during the active period of the day, i.e., after the group has left the morning sleep tree and before the group has arrived at the evening sleep tree. After arriving at the sleep trees, individuals tended to spend time self-grooming, allogrooming, and resting but alert before falling asleep and becoming inactive. I excluded the rest-inactive-sleep records at sleeping sites, but included social and alert records. In the winter, lemurs usually arrived at their sleeping sites earlier (1400-1500h), and data tended to be collected until 1700h. In warmer seasons, lemurs sometimes stayed active until dusk (and even after); I would collect relatively few data at the evening sleep site.

I grouped proportions of behaviors into four main activity categories: feeding (all feeding behaviors), resting (including self-grooming, sitting, sleeping during the day, allogrooming), social behavior (allogrooming, scentmarking, carpal marking, tail anointing, vocalizing, alarm calls, contact calls), and travel (walking, running, leaping, jumping, climbing). Other includes behaviors such as licking dirt or termite trails, drinking water in human areas – very specific behaviors that will be used at a later date for anecdotal descriptions.

To investigate the effects of habitat variables (Reserve vs. Non-Reserve) on various activity variables, I analyzed monthly medians for each group using a Kruskal-Wallis one-way analysis of variance. Correlations between activity budget variables and dietary composition were examined using Spearman rank-order correlation, using monthly blocks.

6.3 Activity Budgets

Overall, ring-tailed lemurs spent the majority of their active time resting (Figure 6.2a). Feeding was also a major activity during the day, followed by travel and then social behavior. The average proportion of active time devoted to the four main activity categories differed among groups (Figures 6.2b, 6.2c, Table 6.1). Reserve Groups spent more time resting, while Non-Reserve Groups devoted more time to feeding. Interestingly, this pattern coincided with differences in time spent traveling. Non-Reserve Groups spent more time traveling than did groups inside the Reserve.

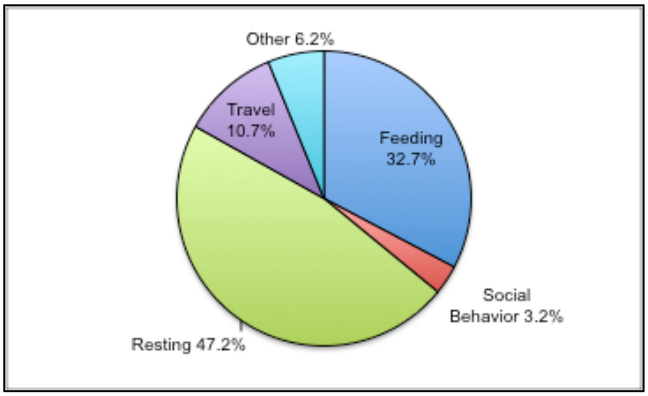


Figure 6.2a Overall percentage activity budget for all four study groups at BMSR.

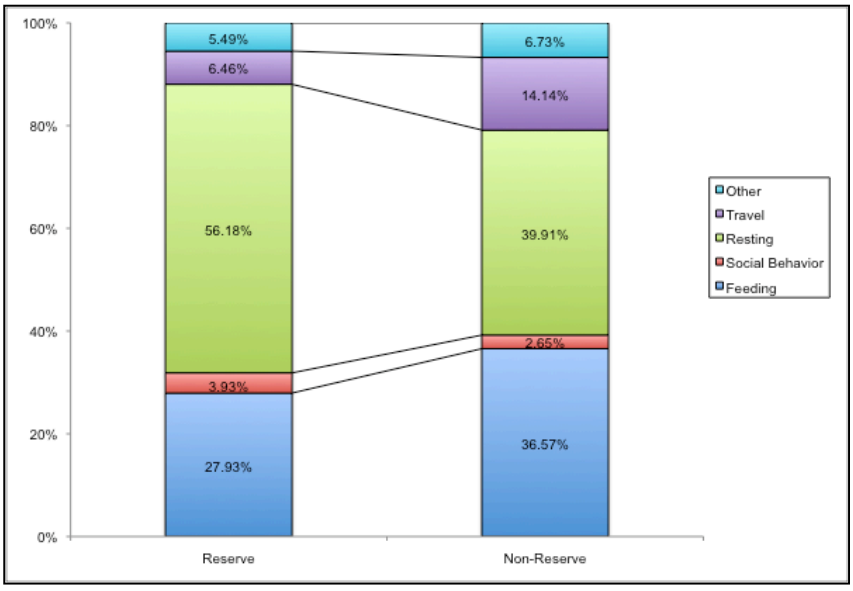


Figure 6.2b Percentage activity budget comparison for Reserve and Non-Reserve Groups.

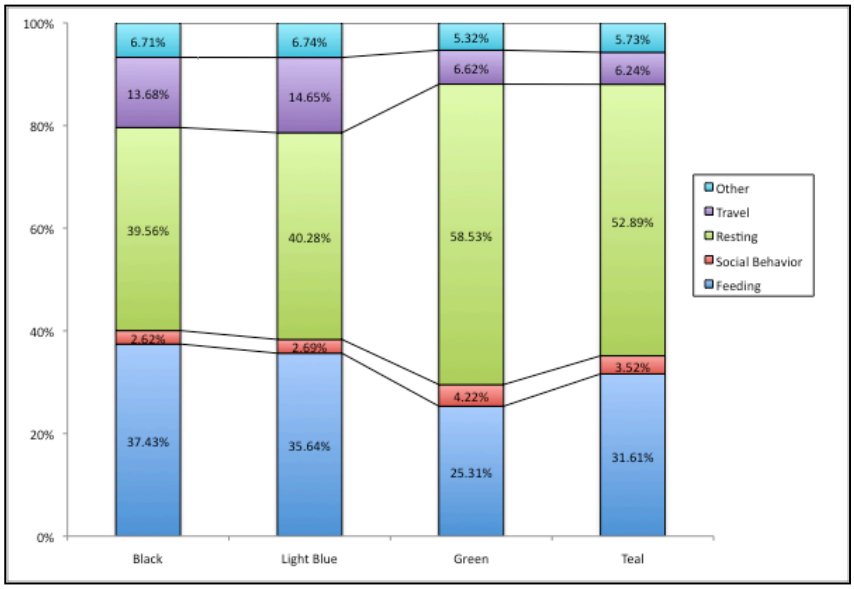


Figure 6.2b Percentage activity budget comparison for all four study groups.

Table 6.1 Comparisons of activity budgets for all four study groups and pooled data.

	Feeding	Social Behavior	Resting	Travel	Other
Black	37.43%	2.62%	39.56%	13.68%	6.71%
Light Blue	35.64%	2.69%	40.28%	14.65%	6.74%
Green	25.31%	4.22%	58.53%	6.62%	5.32%
Teal	31.61%	3.52%	52.89%	6.24%	5.73%
Non-Reserve	36.57%	2.65%	39.91%	14.14%	6.73%
Reserve	27.93%	3.93%	56.18%	6.46%	5.49%
Total	32.25%	3.29%	48.05%	10.30%	6.11%

When groups' activity budgets were examined using the Kruskal-Wallis one-way analysis of variance, two of the four activity categories (rest $p<0.0001$, and travel $p<0.0001$) were found to be significantly different. The amount of time spent in social activities remained fairly consistent among all groups (Table 6.2, Figures 6.3, b).

Groups inside the protected Reserve spent more time resting (Table 6.2, Figures 6.4a, b). There were no significant within-site differences for resting behavior. Finally, overall travel

accounted for significantly more active time in Non-Reserve Groups than in Reserve Groups (Table 6.2, Figures 6.5a, b). There was no significant within-site difference.

Table 6.2 Kruskal-Wallis comparisons of feeding, social behavior, resting, and traveling.

Comparison of time spent in social activities among all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.427	0.5132	N	N
Black vs. Light Blue	0.402	0.5261	N	N
Black vs. Teal	0.349	0.5544	N	N
Green vs. Light Blue	0.110	0.7396	N	N
Green vs. Teal	0.049	0.8246	N	N
Light Blue vs. Teal	0.003	0.9565	N	N
Comparison of time spent feeding/foraging among all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	7.560	0.0060	Y	Y
Black vs. Light Blue	1.221	0.2692	N	N
Black vs. Teal	3.791	0.0515	N	N
Green vs. Light Blue	5.742	0.0166	N	Y
Green vs. Teal	0.995	0.3185	N	N
Light Blue vs. Teal	0.980	0.3221	N	N
Comparison of time spent resting among all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	12.452	0.0004	Y	Y
Black vs. Light Blue	0.006	0.9404	N	N
Black vs. Teal	7.207	0.0073	Y	Y
Green vs. Light Blue	21.193	0.0001	Y	Y
Green vs. Teal	1.438	0.2305	N	N
Light Blue vs. Teal	13.494	0.0002	Y	Y
Comparison of time spent resting among Reserve and Non-Reserve Groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve vs. Non-Reserve	27.325	0.0001	Y	Y
Comparison of time spent traveling among all four study	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**

groups				
Black vs. Green	21.399	0.0001	Y	Y
Black vs. Light Blue	2.022	0.1550	N	N
Black vs. Teal	19.873	0.0001	Y	Y
Green vs. Light Blue	11.598	0.0007	Y	Y
Green vs. Teal	1.499	0.2208	N	N
Light Blue vs. Teal	8.942	0.0028	Y	Y
Comparison of time spent traveling among Reserve and Non-Reserve Groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve vs. Non-Reserve	29.846	0.0001	Y	Y

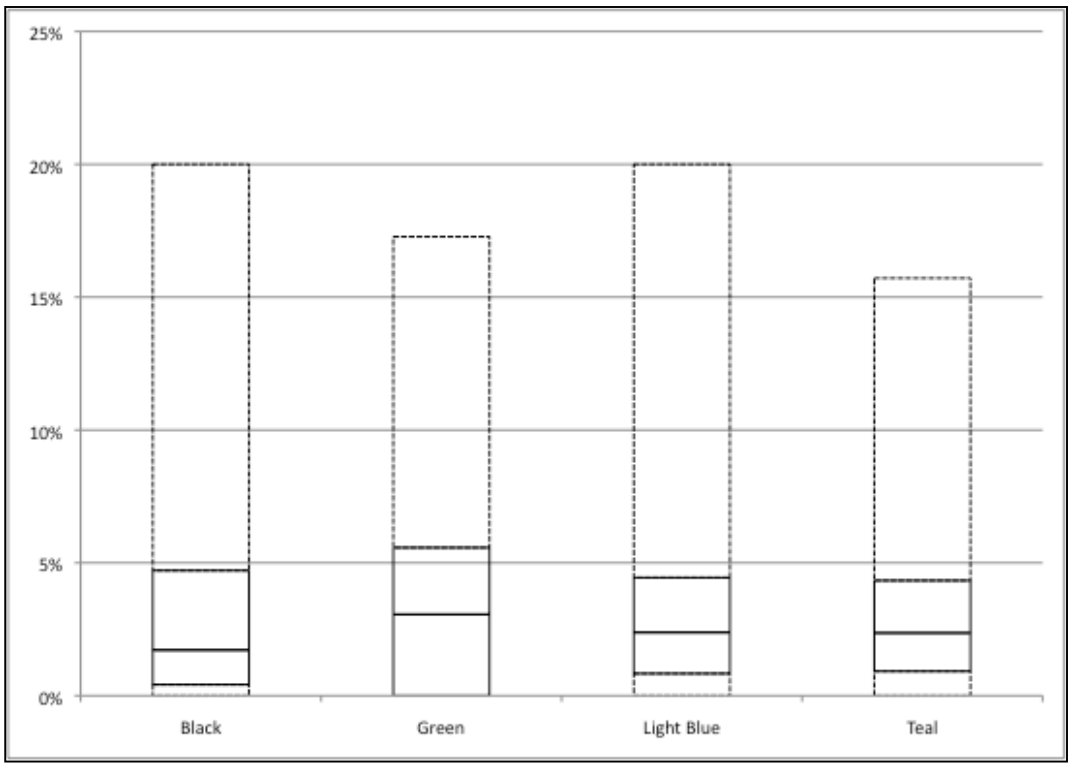


Figure 6.3 Boxplots comparing time spent in feeding activities in all four study groups.

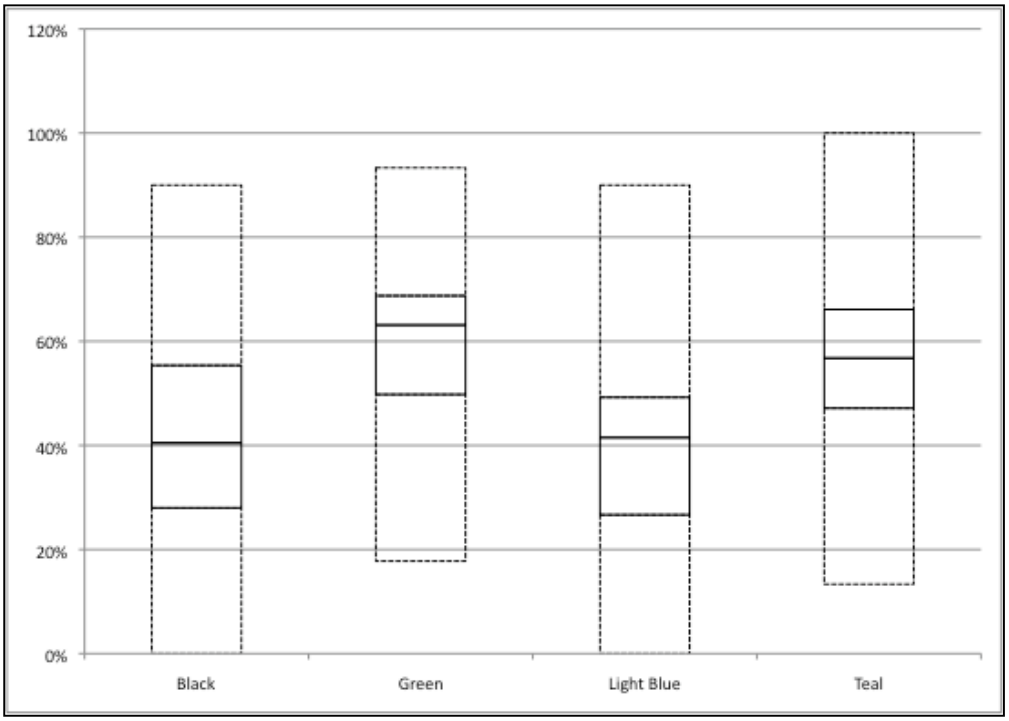


Figure 6.4a Boxplots comparing time spent resting among all four study groups.

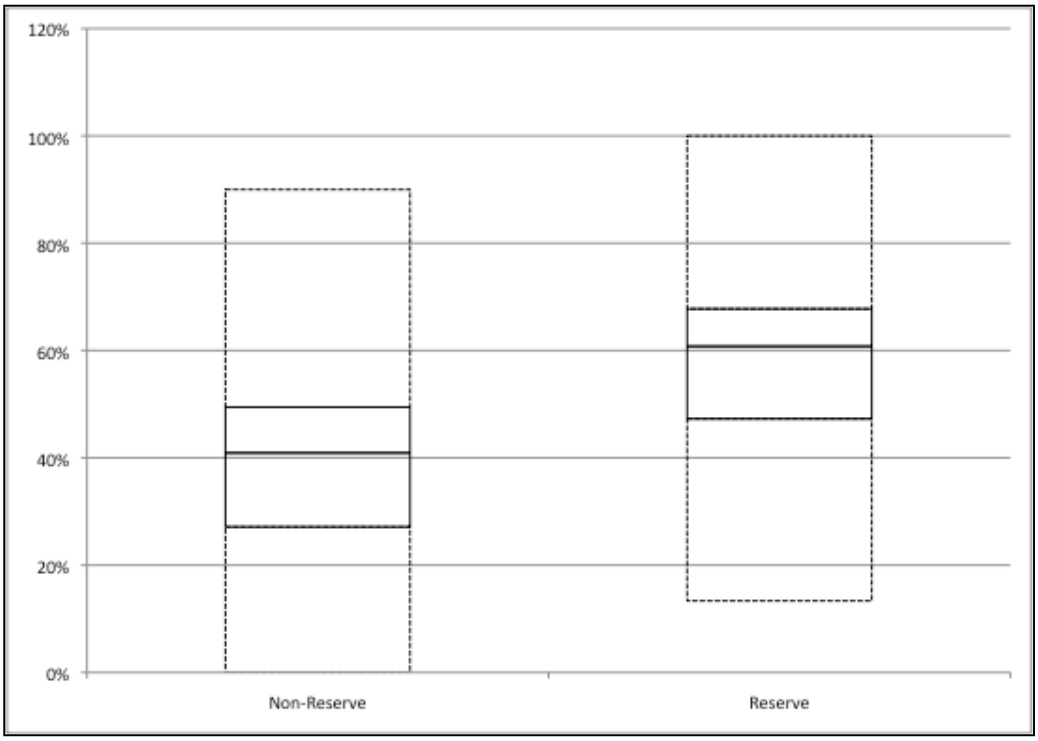


Figure 6.4b Boxplot comparing time spent resting in Non-Reserve and Reserve Groups.

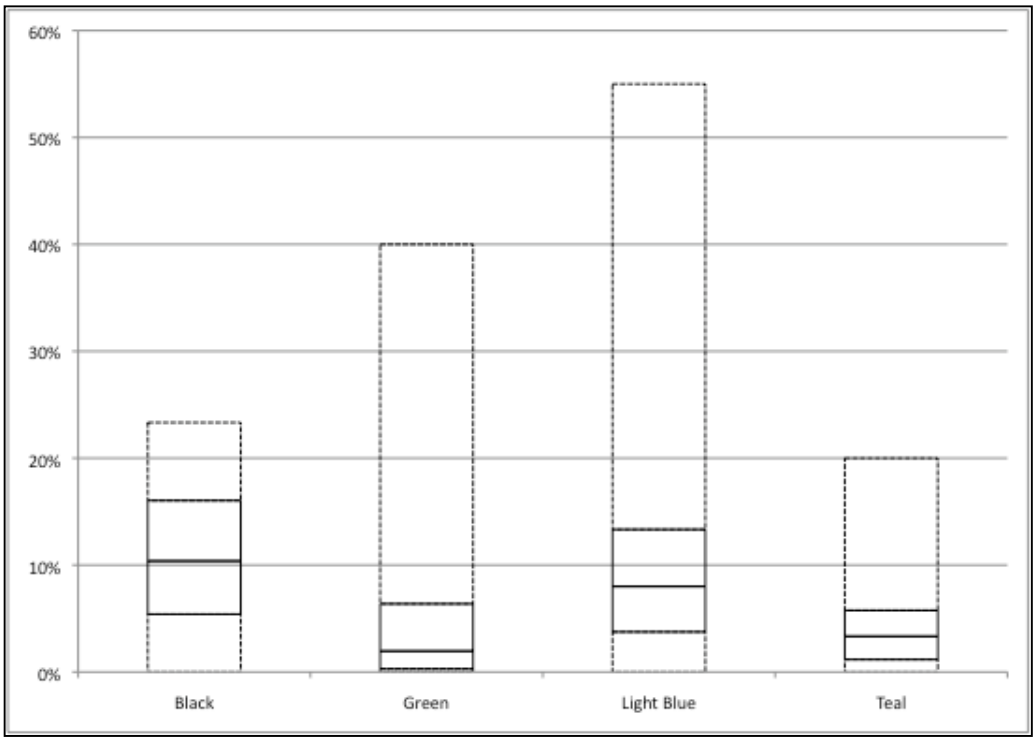


Figure 6.5a Boxplot comparing time spent traveling among all four study groups.

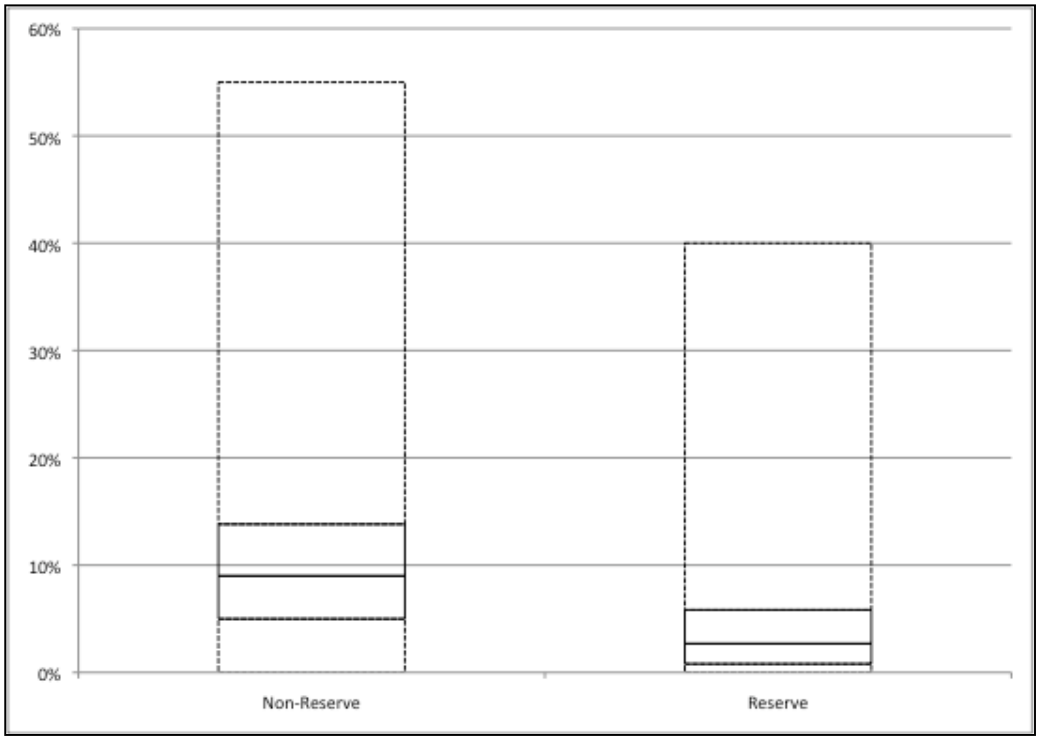


Figure 6.5b Boxplot comparing time spent traveling among Non-Reserve and Reserve Groups.

6.4 Activity Budgets: Seasonality

Each group varies in their time spent in each of the four activity categories throughout the study period (Figures 6.6, 6.7, 6.8, 6.). When each of these categories is examined comparatively between Reserve and Non-Reserve Groups, and all four study groups descriptively, several interesting patterns emerge. Across the seasons, Non-Reserve Groups consistently tended to spend more time feeding (Figure 6.10). When examining each groups' active time spent feeding, several patterns are discernible. For instance, Light Blue Group tended to spend the same portion of its activity budget feeding throughout the study period (Figure 6.11). In contrast, Black Group follows the same peaks and troughs as the Reserve Groups, except they consistently spend more of their active period feeding than Green and Teal Groups (Figure 6.11). This indicates, again, that Black may experience a buffering effect from the Reserve. As was clear with the quantitative analysis, all groups spend similar amounts of time participating in social behavior throughout the study period (Figures 6.12, 6.13). In terms of resting, Green and Teal Groups spend considerable time resting consistently throughout the study period, except in the very beginning of the wet season (Figures 6.14, 6.15). In contrast, Black and Light Blue Groups vary their time spent resting: with longer rest times in the height of the wet season and the mid-dry season of May and June and periods of less resting early in the wet season. There is considerable within site consistency in the amount of time spent traveling (Figures 6.16, 6.17). Reserve Groups appear to travel slightly more during drier months while Non-Reserve Groups sporadically 'spiked' and decreased in the amount of time spent traveling throughout the study period.

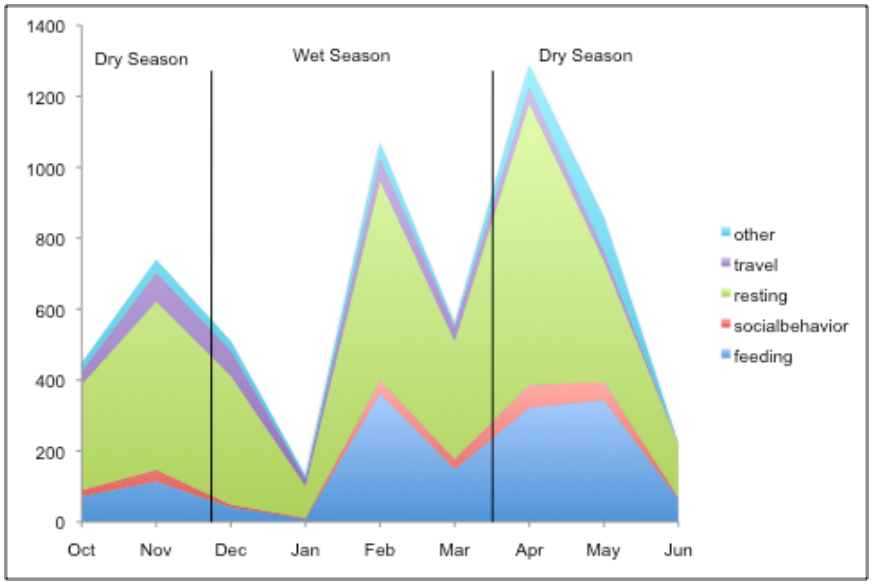


Figure 6.6 Green Group's frequency of feeding, resting, traveling, and in social activities by month. Y-axis is number of times recorded.

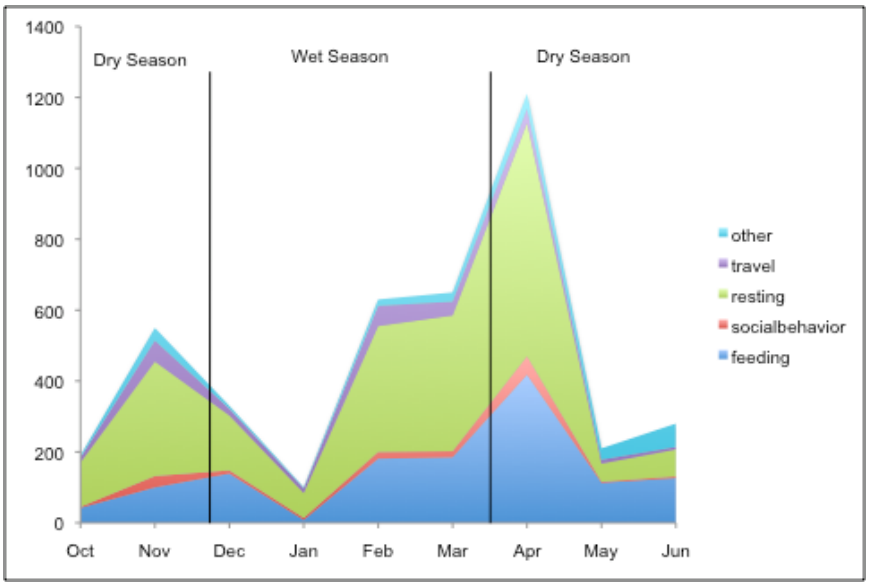


Figure 6.7 Teal Group's frequent of feeding, resting, traveling, and in social activities by month. Y-axis is number of times recorded.

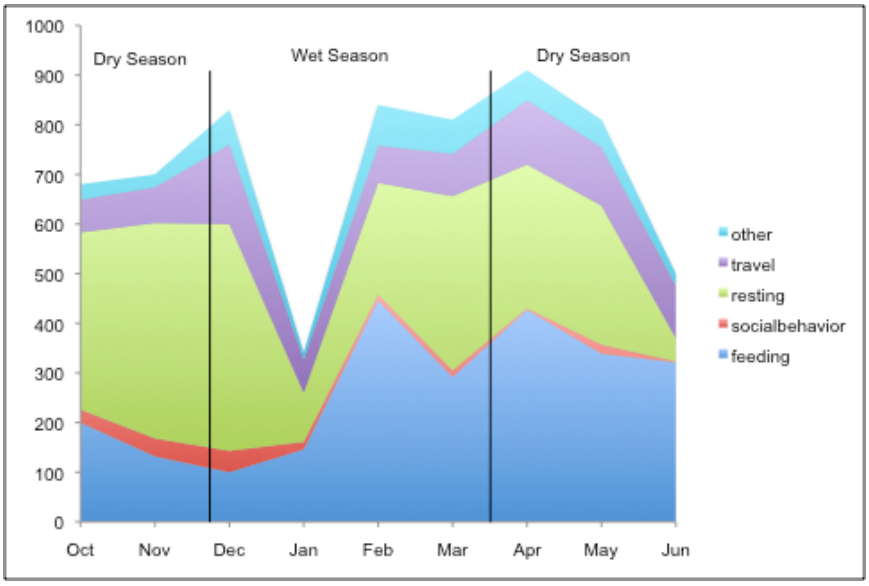


Figure 6.8 Black Group's frequency of feeding, resting, traveling, and in social activities by month. Y-axis is number of times recorded.

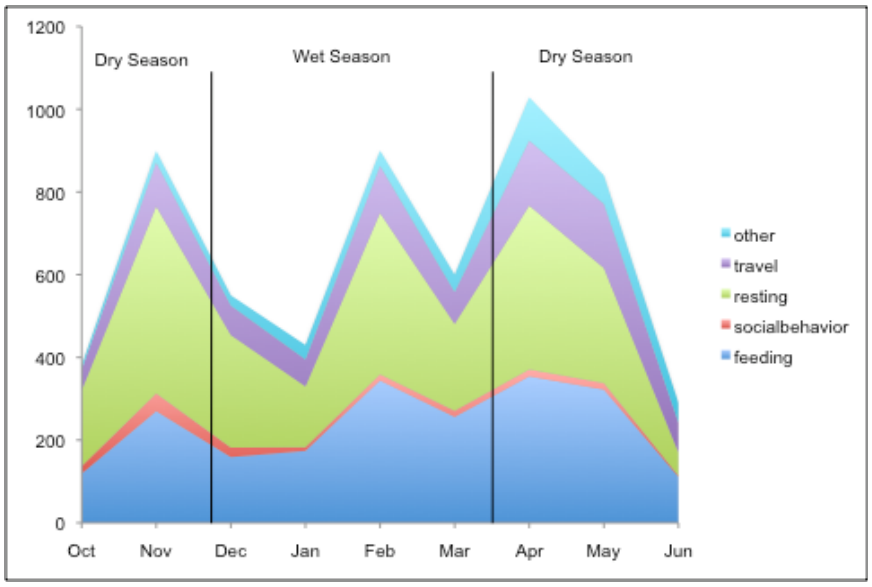


Figure 6.9 Light Blue Group's frequency of feeding, resting, traveling, and in social activities by month. Y-axis is number of times recorded.

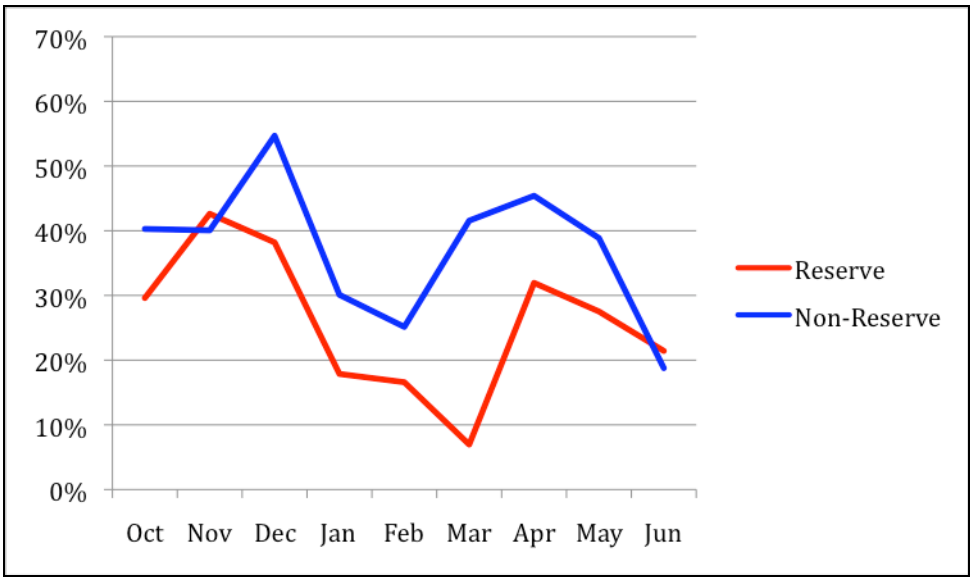


Figure 6.10 Percent of active time spent feeding for Reserve and Non-Reserve Groups each month.

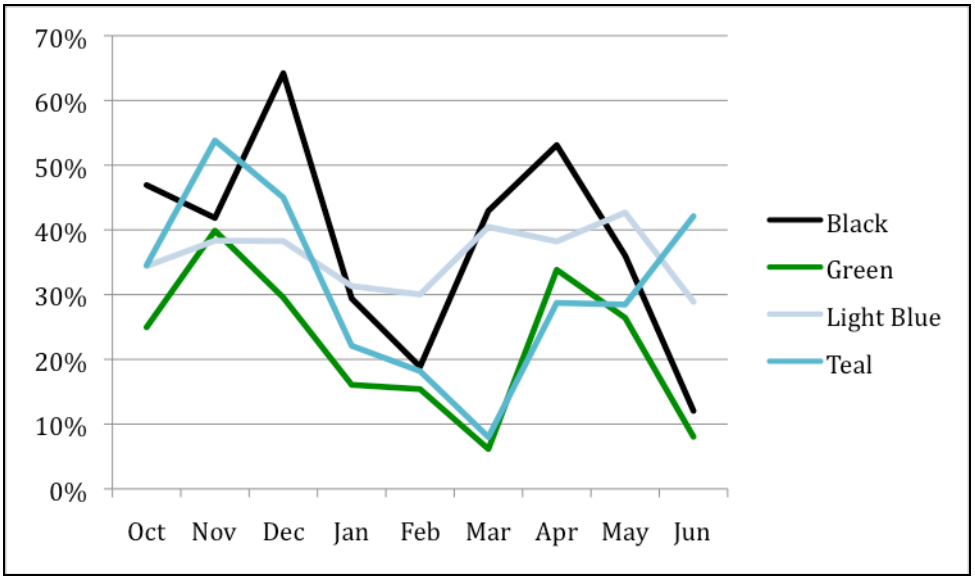


Figure 6.11 Percent of active time spent feeding for all four study groups each month.

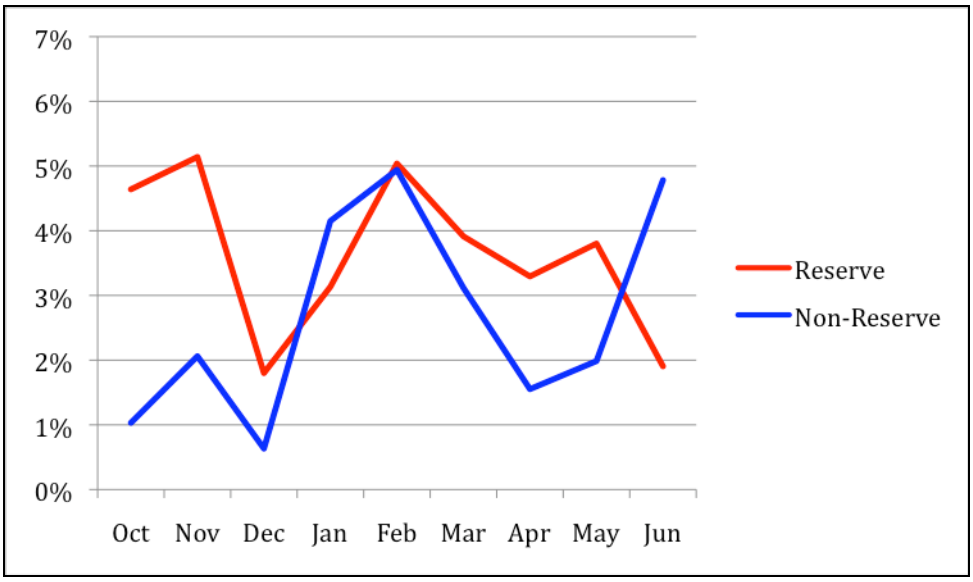


Figure 6.12 Percent of active time in social activities for Reserve and Non-Reserve Groups each month.

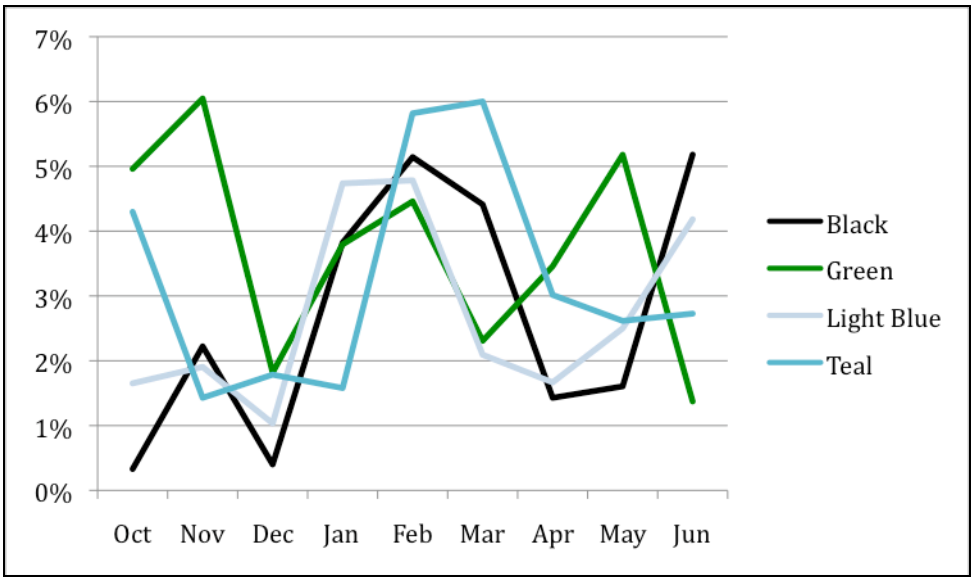


Figure 6.13 Percent of active time in social activities for all four study groups each month.

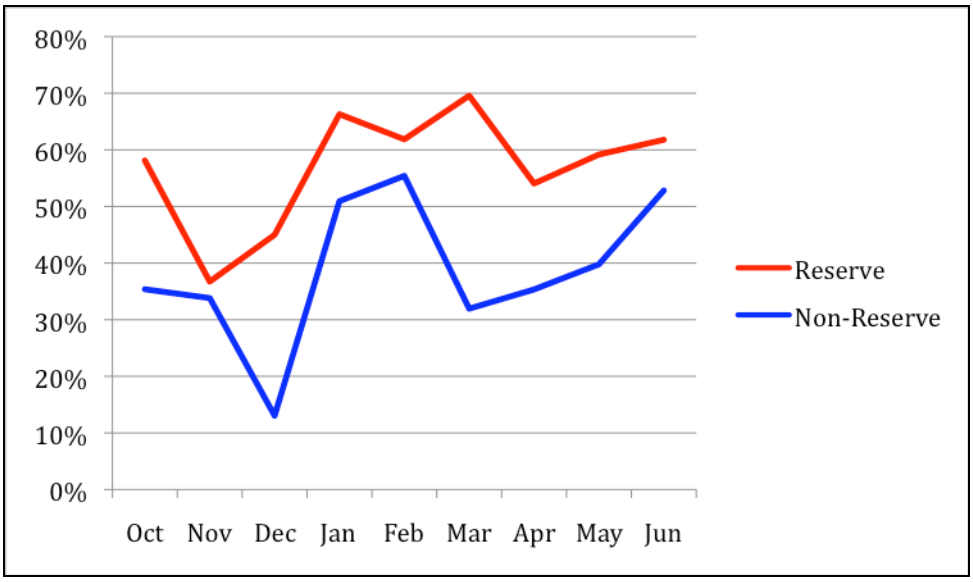


Figure 6.14 Percent of active time spent resting for Reserve and Non-Reserve Groups.

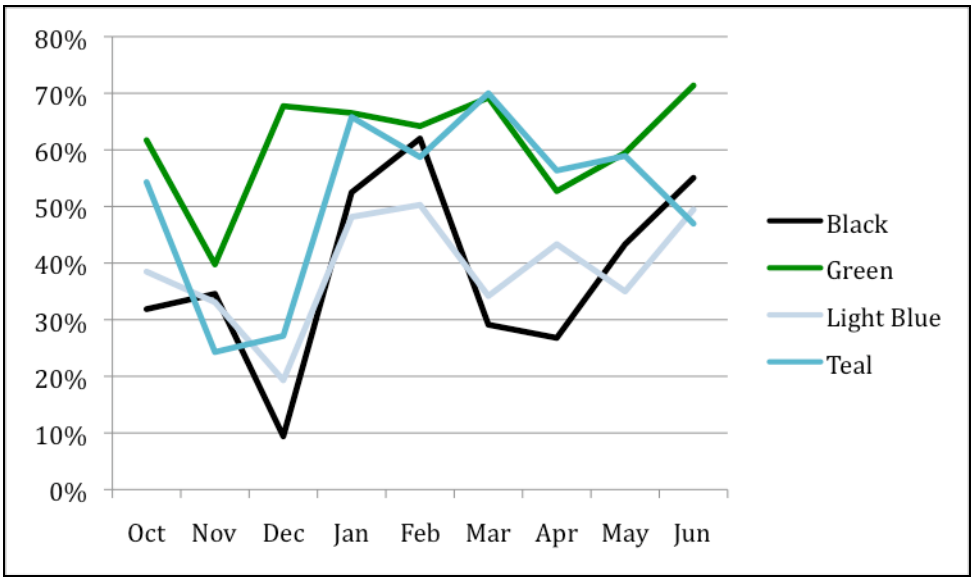


Figure 6.15 Percent of active time spent resting for all four study groups each month.

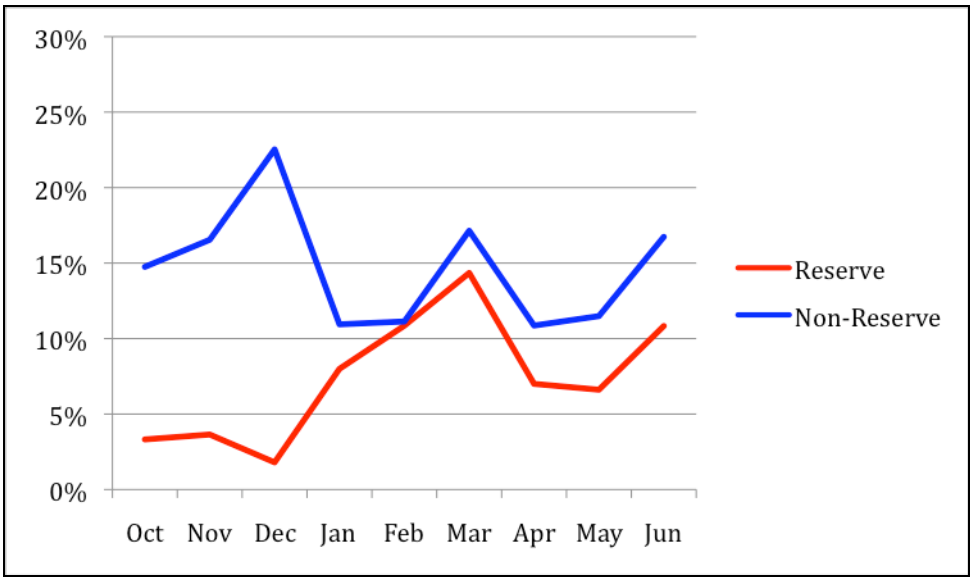


Figure 6.16 Percent of active time spent traveling in Reserve and Non-Reserve Groups each month.

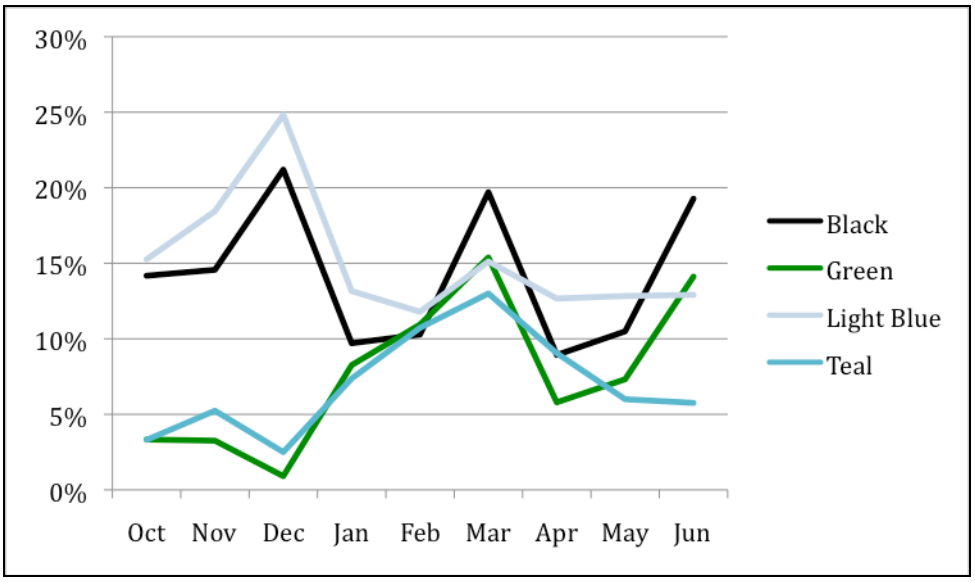


Figure 6.17 Percent of active time spent traveling in all four study groups each month.

6.5 Activity Budgets: Traveling

During the study period, it quickly became obvious that Non-Reserve Groups spent considerable time running on the ground in their respective habitats. Indeed, it became difficult to follow them at times. Similar to their significantly higher amount of active time spent traveling overall, Non-Reserve Groups spent significantly more time both walking and running

on the ground, particularly Black Group (Figures 6.18a and b, 6.19a and b, Table 6.3). Quantitatively, Black and Light Blue Groups spent significantly more of their active time during the day walking than Green Group, and significantly more of their active time during the day running than either Light Blue or Green Group (Table 6.3; Figures 6.20a, b; Figures 6.21a, b). Arboreal travel, while more costly, occurred rarely and therefore was not analyzed.

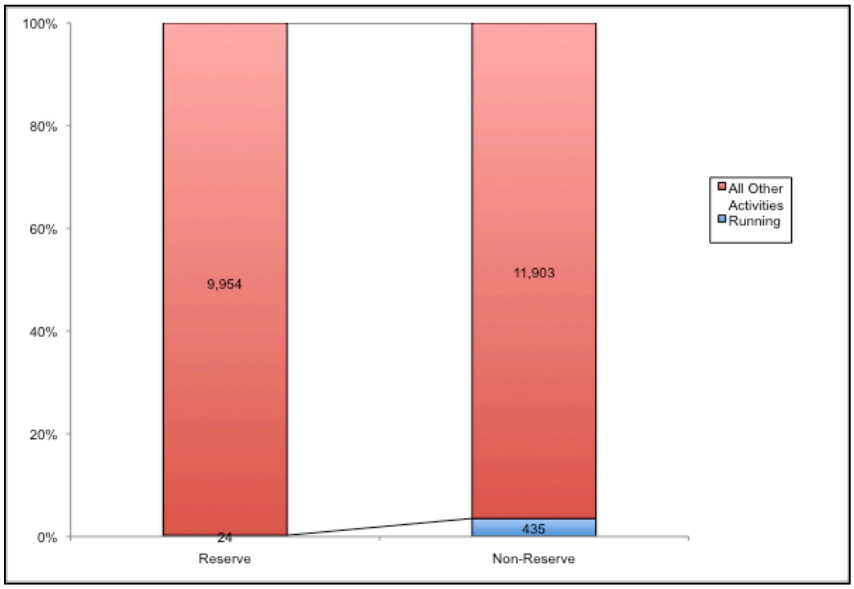


Figure 6.18a Percent of active time spent running in Reserve and Non-Reserve Groups.

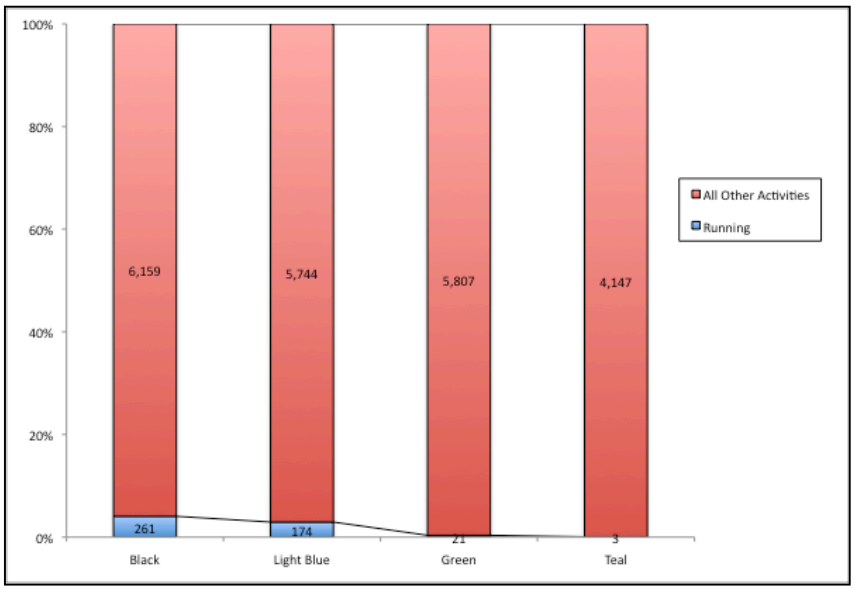


Figure 6.18b Percent of active time spent running in all four study groups.

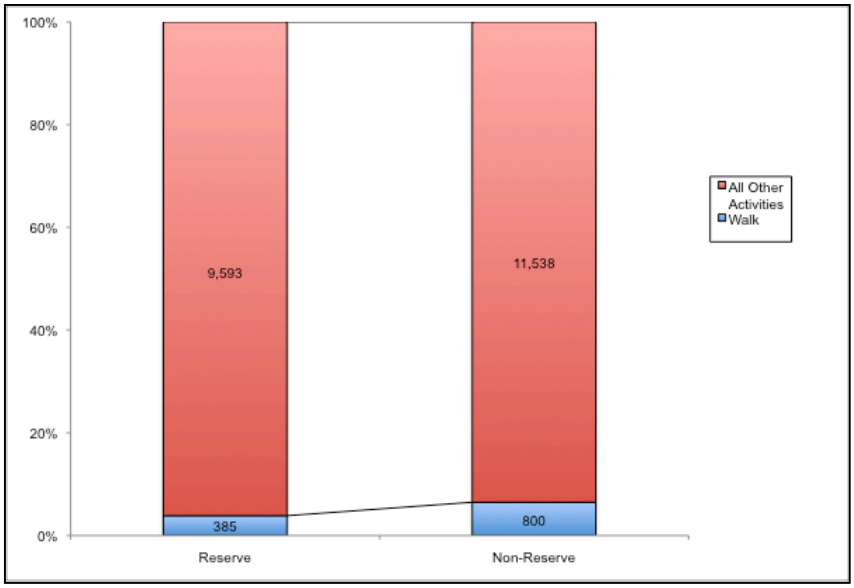


Figure 6.19a Percent of active time spent walking in Reserve and Non-Reserve Groups.

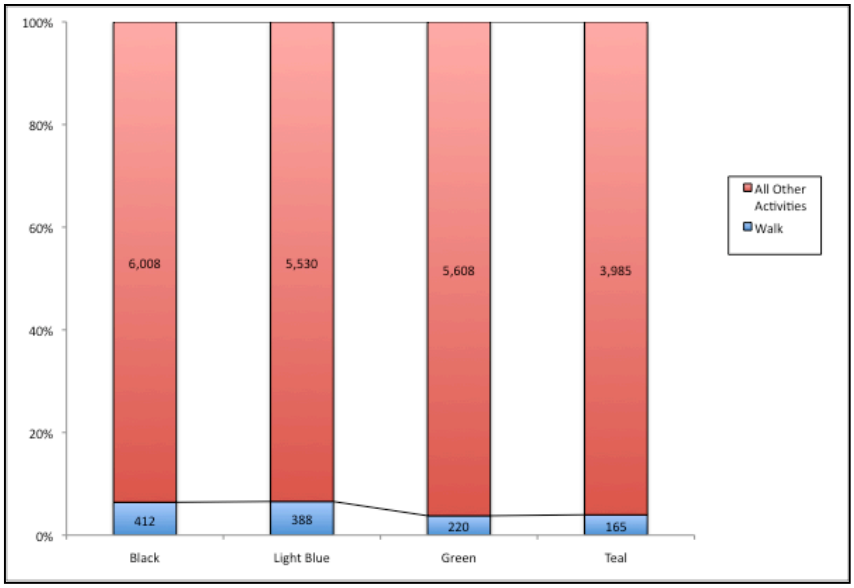


Figure 6.19b Percent of active time spent walking in all four study groups.

Table 6.3 Kruskal-Wallis comparisons of active time spent running and walking between Reserve and Non-Reserve, and all four study groups.

Comparison of active time spent running between all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	39.981	0.0001	Y	Y
Black vs. Light Blue	3.959	0.0466	N	Y
Black vs. Teal	42.353	0.0001	Y	Y
Green vs. Light Blue	25.222	0.0001	Y	Y
Green vs. Teal	1.561	0.2115	N	N
Light Blue vs. Teal	29.873	0.0001	Y	Y
Comparison of active time spent running between Reserve and Non-Reserve Groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve and Non-Reserve Groups	67.331	0.0001	Y	Y
Comparison of active time spent walking between all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	7.985	0.0047	Y	Y
Black vs. Light Blue	0.004	0.9509	N	N
Black vs. Teal	2.863	0.0906	N	N
Green vs. Light Blue	7.670	0.0056	Y	Y
Green vs. Teal	2.377	0.1231	N	N
Light Blue vs. Teal	2.417	0.1201	N	N

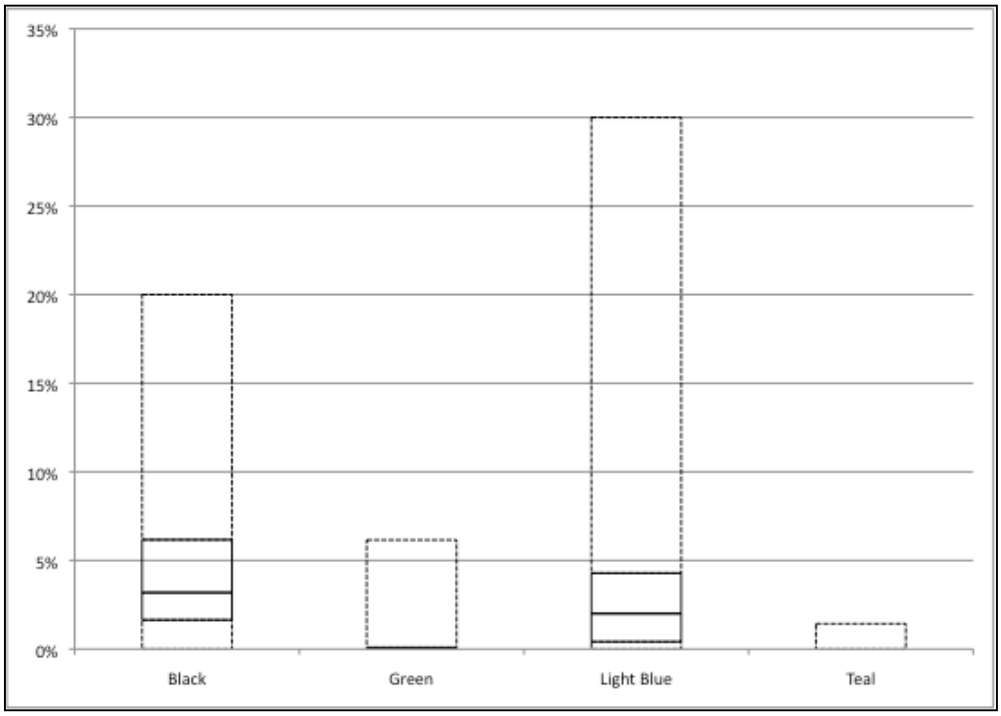


Figure 6.20a Boxplot comparison of active time spent running in all four study groups.

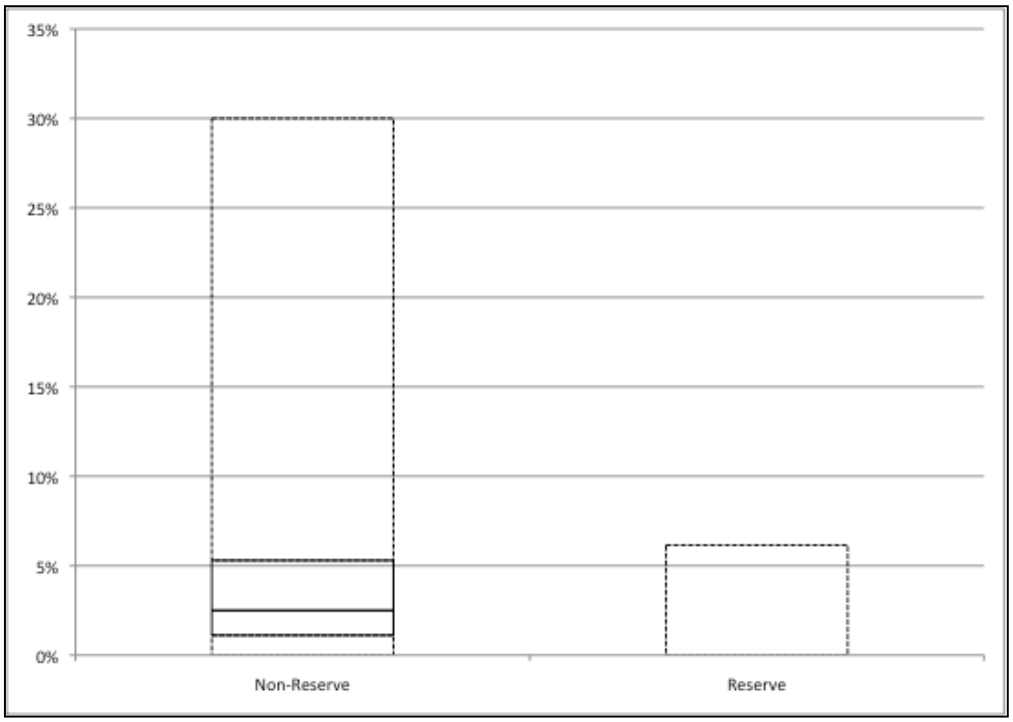


Figure 6.20b Boxplot comparison of active time spent running in Reserve and Non-Reserve Groups.

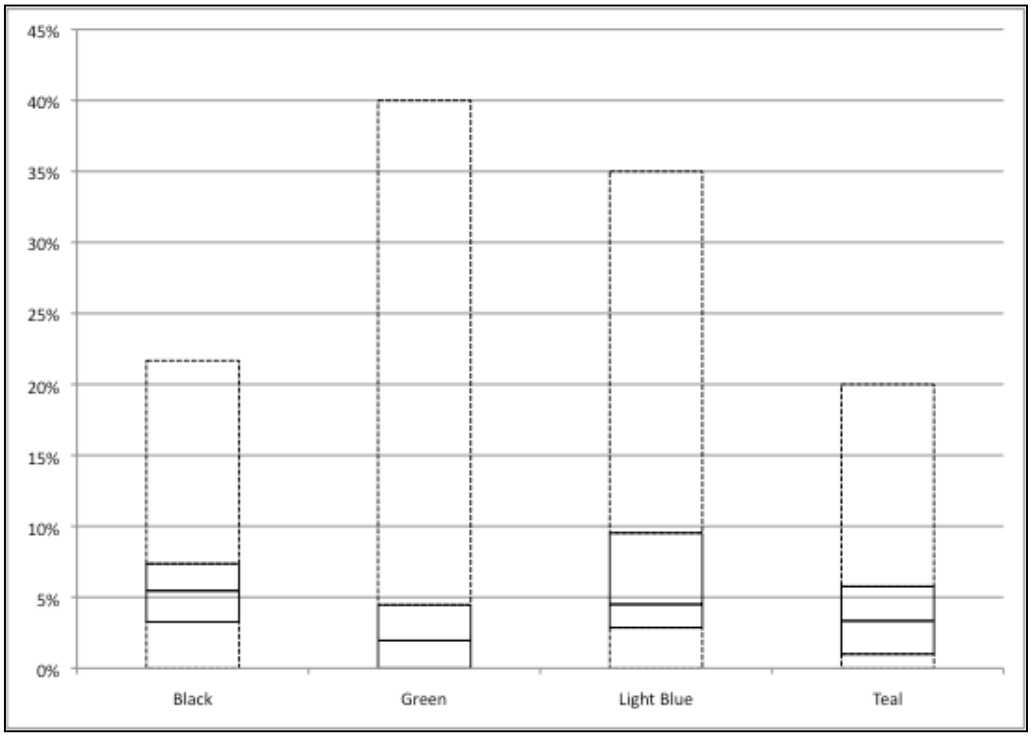


Figure 6.21a Boxplot comparisons of active time spent walking among all four study groups.

6.6 Effect of Diet on Activity Patterns

Several dietary composition variables were found to affect activity budgets and several site-specific differences (Table 6.4). For example, Non-Reserve Groups' leaf consumption was negatively correlated with time devoted to travel, but this was not the case for Reserve Groups; an indication that Reserve Groups were able to exploit terrestrial herbs more readily than Non-Reserve Groups. Reserve Groups were able to remain more sedentary and feed on large patches of high-quality leaves, as opposed to Non-Reserve Groups that moved throughout their range and fed more on fruits. Similarly, Reserve Groups showed a strong negative relationship between the amount of time spent resting and fruit consumption, however, the relationship was not as strong for Non-Reserve Groups. The same pattern exists for resting and leaf consumption. This indicates a difference in behavioral patterns for Non-Reserve and

Reserve Groups: Reserve Groups are resting more and still consuming the same amount and types of food resources. The amount of time spent traveling was more negatively correlated to dietary diversity for Non-Reserve Groups than for Reserve Groups. This suggests that while Non-Reserve Groups are traveling more, it is not making a significant contribution to their dietary diversity.

The amount of time spent feeding correlated more strongly to fruit consumption in Reserve Groups than in Non-Reserve Groups. The same relationship existed for leaf consumption. In fact, time spent feeding was slightly negatively correlated for Non-Reserve Groups. Finally, for Reserve Groups, time spent traveling was strongly negatively correlated to time spent feeding. This pattern was not evident for Non-Reserve Groups. The fact that these relationships are different among the Reserve and Non-Reserve Groups is an indication that these groups use different strategies, activity budgets, and forest resources on a daily basis to acquire necessary resources. Additionally, the fact that more fruit feeding is connected to less resting for both groups indicates the patchy nature of this particular resource for all groups.

Table 6.4 Results of Spearman's Rank correlation coefficient on activity budget and diet variables. A single asterisk indicates that the probability that the two variables are independent is less than 5%. A double asterisk indicates that the probability that the two variables are independent is less than 1%.

Variables	All		Reserve		Non-Reserve	
	Spearman's Rank Correlation Coefficient	Probability that the two variables are independent	Spearman's Rank Correlation Coefficient	Probability that the two variables are independent	Spearman's Rank Correlation Coefficient	Probability that the two variables are independent
Daily Percent of Time Spent Traveling vs. Daily Total Fruit Consumption	0.0124	0.8750	-0.1701	0.1365	0.0944	0.3901
Daily Percent of Time Spent Traveling vs. Daily Total Leaf Consumption	0.0311	0.6935	-0.0130	0.9098	0.0080	0.9418

Daily Percent of Time Spent Traveling vs. Daily Total Number of Species in Diet	-0.0657	0.4046	-0.2072	0.0687	0.0138	0.9003
Daily Percent of Time Spent Resting vs. Daily Total Fruit Consumption	-0.4082	0.0000**	-0.3186	0.0045**	0.4404	0.0000**
Daily Percent of Time Spent Resting vs. Daily Total Leaf Consumption	-0.1969	0.0118*	-0.2669	0.0182*	0.0562	0.6097
Daily Percent of Time Spent Resting vs. Daily Total Number of Species in Diet	-0.0950	0.2278	-0.1069	0.3518	0.0334	0.7615
Daily Percent of Time Spent Feeding vs. Daily Total Fruit Consumption	0.4541	0.0000**	0.5141	0.0000**	0.4093	0.0001**
Daily Percent of Time Spent Feeding vs. Daily Total Leaf Consumption	0.3617	0.0000**	0.4360	0.0001**	0.2777	0.0101*
Daily Percent of Time Spent Feeding vs. Daily Total Number of Species in Diet	0.3109	0.0001**	0.3794	0.0006**	0.2497	0.0212*
Daily Percent of Time Spent Feeding vs. Daily Percent of Time Spent Traveling	-0.0762	0.3335	-0.1683	0.1407	0.0718	0.5140

6.7 Discussion

Anthropogenic habitat disturbance appears to have had some important effects on activity patterns among the ring-tailed lemurs at Beza Mahafaly. In general, Non-Reserve Groups spend more of their active time both feeding and traveling than groups inside the Reserve. Non-Reserve Groups devoted less of their time to resting compared to Reserve Groups. When examining changes across seasons, Reserve Groups tend to rest more during the lean months whereas Non-Reserve Groups tend to feed and travel more, at the expense of time spent in social behavior such as grooming. These patterns are consistent with some of the feeding data: Reserve Groups consumed less fruit in the dry season as they rested more. However, data also indicated that Non-Reserve Groups have to maintain a more active activity to maintain adequate resource acquisition.

There are also several significant differences in the traveling data among Reserve and Non-Reserve Groups. Non-Reserve Groups consistently traveled more throughout the year, whereas Reserve Groups had small peaks at the transition to the wet season in November and at the peak of the wet season in February. Not only did Non-Reserve Groups travel more, they traveled differently, literally at a run. This energetically demanding form of locomotion indicates more stressful circumstances as they encounter a higher incidence of open canopy and perhaps more predators, while at the same time lacking habitat structure that enables safer travel.

This result, coupled with the feeding differences, indicates that Non-Reserve Groups spent more time feeding due to smaller resource size (causing slower net intake rates, and more time traveling due to smaller patch sizes), resulting in the animals needing to travel and visit more patches each day. Earlier chapters have discussed how Non-Reserve Groups consume a higher diversity of foods, while Reserve Groups focused on presumably higher quantities of

fewer species. Moreover, Non-Reserve Groups tended to spend more time foraging as they are focused on feeding. These results indicate that food patches may be larger with larger fruits, more predictable, and adequate for groups inside the Reserve. On the other hand, Non-Reserve Groups may be forced to negotiate the demands of living in a more degraded habitat by feeding and traveling more.

Dunbar (1992) showed that ecologically stressed baboons tended to increase feeding time, and decrease resting and social time. More recently, this same pattern was found in groups of diademed sifaka inhabiting fragmented forests in eastern Madagascar (Irwin 2006), and in ring-tailed lemurs at BMSR (Sauther et al. 2006). This is also consistent with changes found in Non-Reserve ring-tailed lemurs around BMSR, suggesting that they are under ecological stress. The long-term consequences of these differences, and whether these behavioral shifts cause changes in fitness, remain to be seen. Increased resting period has been noted for primates living in low-resource environments, and those living in human-modified habitats (Estrada et al. 1991, Marsh 1981, MeNon and Poirier 1996). It appears that flexibility is key to how primates negotiate their habitats and that individuals will alter the amount of time allotted to behaviors based on the surrounding ecological variables. In the case of Non-Reserve ring-tailed lemurs at BMSR, spending more time feeding and traveling to access food resources is a viable strategy in the short term. It is evident that patterns of energy expenditure and resource acquisition differ between, and within, primate species.

In general, anthropogenic habitat disturbance at BMSR appears to have affected ring-tailed lemurs' activity patterns and budgets. Ongoing research documenting demographic shifts will provide information on whether or not these changes will have a serious impact on survival outside the small, protected Reserve. Observations in this study do appear to be symptomatic of

other serious ecological shifts, which may have severe impacts on survival. Several lines of evidence suggest that ring-tailed lemurs outside of the Reserve have a more energetically stressful activity pattern: 1.) Non-Reserve Groups focused on smaller patches of food that required more foraging time, and more traveling, while groups inside the Reserve focused on larger patches; 2.) energetically costly activities such as traveling and running, were greatly increased in Non-Reserve Groups. It is possible that the dietary shifts underlying the changes in activity, more feeding and more traveling, could possibly be the more relevant threat.

Further research is required to understand more thoroughly the long-term viability of ring-tailed lemurs inhabiting the anthropogenically disturbed habitats around BMSR. Specifically, it will be imperative to continue the examination of physiological effects of altered diets such as effects on health and body condition, the prevalence of disease, demographic constraints including changes in fertility and fecundity, and alterations to dispersal rates (which has been recorded at BMSR since 2003, Sauther and Cuozzo 2009). It appears that ring-tailed lemurs are exhibiting behavioral flexibility and have the capacity to alter traveling patterns, feeding and foraging strategies, and dietary strategies. The long-term costs of this flexibility must be assessed in order to know the viability of ring-tailed lemurs in altered habitats. With the knowledge that few forests in Madagascar remain untouched by human activity, a more thorough understanding of the sustainability of populations in disturbed forests will prove useful to assessing conservation status of populations outside protected areas and producing the most effective conservation plans for species with the highest degree of risk.

CHAPTER 7

EFFECTS OF ANTHROPOGENIC HABITAT DISTURBANCE ON *LEMUR CATTA*: SOCIAL BEHAVIOR

7.1 Introduction

7.1.1 Anthropogenically disturbed habitats and social behavior

A lack of long-term, intensive studies of social behavior has presented a gap in the primatogical literature. While several studies have examined the effects of anthropogenically altered habitats on activity budget (Chapter 6, Estrada et al. 1999, Irwin 2006, Menon and Poirier 2006, Onderdonk and Chapman 2000, Tutin 1999), there has been almost no examination of the effects of these types of habitat disturbances on social behaviors in primates.

While very little examination has been made into whether habitat disturbance can alter social behaviors, the possibility certainly exists. There are four variables that have been identified as important factors in changing social behaviors in altered habitats (Irwin 2006). First, demographic changes, such as altered dispersal patterns, higher mortality or injury rates, will change the number of social partners in a group and thus may change social behaviors and their rates in a group. Second, dietary changes in altered habitats may affect groups in several ways. Directly, individuals may respond with different social patterns via altered interindividual and intergroup spacing during feeding, and changes in ranging patterns that may alter groups' spacing during feeding. Indirectly, dietary changes may affect a population's social behavior due to reduced energetic capacity with a poorer quality diet. Energetically demanding behaviors, such as play, may be curtailed or eliminated. Furthermore, if the number of individuals most likely to engage in certain activities such as play, e.g. infant and juvenile classes, is reduced due to lack of adequate resources or higher rates of predation, then it will affect the frequency of such behaviors. Third, if dietary resources affect the health and immune systems of individuals, these

health differences might respond either through reductions in activity or increase in behaviors that mitigate disease transmission (e.g. grooming, Loudon 2009). Finally, the proximity to neighboring groups, due to alterations in suitable habitat, will affect the frequency and nature of intertroop encounters, probability of extratroop matings, and dispersal to neighboring groups of non-local individuals.

7.1.2 Background information: Social Behavior of *Lemur catta*

Intragroup behavior – Ring-tailed lemur groups have been well studied by a variety of researchers since the 1960s (Gould et al. 1999, Gould 2006, Jolly 1966, Koyama et al. 2006, Sauther 1992, Gould 1994, Sauther 1998, Sauther et al. 1999, 2002, Sauther and Cuozzo 2009, Sussman 1972). Throughout their geographic range, groups tend to have relatively stable structure consisting of a several related adult females; their offspring including infants and juveniles; a few central males who tend to stay in closer proximity to females than other males (but can also disperse eventually); and some peripheral males, who will disperse, probably several times throughout their lives, when they mature (Gould 1997, Jolly 1966, Sauther 1992, Sauther et al. 1999, Sussman 1992). Groups tend to become unstable when troops become too large, usually around 20 individuals, resulting in fission (Gould et al. 2003; Jolly et al. 2002; Koyama 1991; Koyama et al. 2002; Sussman 1991; Taylor and Sussman 1985). Average group size at Beza is 10.4 individuals but ranges from 3 – 20 individuals (Sauther and Cuozzo, 2009), whereas group size averages at other sites range from 9-22 individuals (Budnitz and Dainis, 1975, Jolly 1966, Sussman 1974,). In terms of social structure, although females are clearly dominant in resource competition and agonistic interactions most of the time (Budnitz and Dainis 1975, Jolly 1966, Kappeler 1990, Taylor 1986), these dominance relationships are dynamic and can change over time (Sauther 1992). Additionally, both sexes have linear

dominance hierarchies. Time spent in social activities ranges from 2.6% in one study (Gould 1994) to 8.6 % (Sussman 2004), the highest of any diurnal prosimian. Gould (1994) reported affiliative behavior 1.9% of the time, and 0.3% of social time as agonistic. Sussman (2004) documented 7.1% if social time as affiliative and 1.4% as agonistic. Previous research at Beza has shown individuals spending between 5-11% of their time grooming (allo- or autogrooming), and lower ranking individuals tend to spend more time grooming (Sauther 1992).

Scentmarking – Scentmarking is almost ubiquitous among lemurs and other strepsirhines (Gould and Overdorff 2002, Kappeler 1998, Mertl-Millhollen 2000, Petter et al. 1977). Olfactory signals can convey such information as identity of species, group, gender, reproductive condition, and even individuals (Harrinton 1977, Mertl 1975, Schilling 1979, Ziegler et al. 1993). Additionally, other research has found that special functions of scentmarking include territoriality (i.e. marking the boundaries of territories; e.g. Charles-Dominique 1977; Mertl-Millhollen 1979, 2000), communicating information regarding reproductive behavior (e.g. Epple et al. 1986), and functions correlating with inter or intragroup agonism, aggression, and dominance (Epple 1986, Irwin et al. 2004, Irwin 2006, Kappeler 1990, 1998, Ralls 1971, Schilling 1979).

Olfactory communication appears to be heavily relied upon by ring-tailed lemurs, who scent mark trees and saplings throughout their range (Mertl-Millhollen 2000, Loudon 2009). Among ring-tailed lemurs, females use anogenital glands and males use both anogenital, sternal, and carpal glands (Sauther et al. 1999) to establish and maintain territorial boundaries (Mertl-Millhollen et al. 2006) as well as communicate social sexual components and functions (Gould and Overdorff 2002). Scentmarking may serve mainly as in intergroup communication (Irwin et al. 2004, 2006).

A significant advantage of scentmarking in intergroup dynamics is its significant lower energetic demand compared to agonistic behaviors serving the same function: establishing territories (Gosling 1990). In this manner, scentmarking may serve as a mechanism for trespassers to avoid direct conflict. Furthermore, scentmarking is an effective method of advertising a group's presence and broadening a group's communication impact in both space and time, than either visual displays or vocalizations (Gorman 1990). This is especially effective for territorial defense in species with larger home ranges with poor visibility in closed or dense habitats, both less conducive to long-range visual cues (Irwin 2006).

Intergroup behavior – Ring-tailed lemurs maintain relatively stable territories (Gould et al. 2003, Gould 2006, Sauther et al. 1999). Typically dominant females are the primary participants in intergroup agonism (Pride et al. 2006, Sauther 1993). As the number of adult females increases in a group, so do the number of intergroup conflicts (Pride et al. 2006). These encounters usually involve varying degrees of scentmarking (anogenitally and carpally), displacements, lunges, and physical contact (Pride et al. 2006). At Berenty, groups tend to lose the encounter if they are venturing outside their range. The outcome of an encounter is not dependent on group size (even small groups can win an encounter), but the energetic costs of attaining a win are lower in larger groups (Pride et al. 2006). At Beza and Berenty, intergroup encounters are common and escalate in frequency during weaning of infants, early lactation, and the dry season (Gould 1989, Jolly 1972, Jolly et al. 1993, Jones 1983, Sauther 1992, Sauther et al. 1999, Sussman 1972, 1977).

7.1.3 Objectives

This chapter focuses on the effects of anthropogenic habitat disturbance on the social behavior of ring-tailed lemurs, *Lemur catta*. Ring-tailed lemurs have been recorded inhabiting

very small forest fragments and discontinuous habitats, however, long-term viability and success of these populations remains unknown. Previous chapters have documented and explained how anthropogenic habitat disturbance around Beza Mahafaly Special Reserve affects the habitat structure and forest composition, causes alterations in feeding ecology, ranging patterns, and activity budgets of ring-tailed lemurs. This chapter will focus on whether anthropogenic habitat disturbance affect intragroup spacing, cohesion, and patterns of affiliation, the nature of affiliative behaviors such as play and grooming, levels of aggression within groups the nature of scentmarking behaviors and/or the frequency of intragroup encounters.

The answers to these questions will provide a more thorough understanding of ring-tailed lemur ecology in disparate habitats, thereby allowing for more informed management decisions in the future. In the bigger picture, this study will provide more data towards creating a better understanding of why some primate species tolerate anthropogenic habitat disturbance and persist, while others do not. A more thorough understanding of how ecological changes can affect the social context of primate groups and the ways in which disturbance-induced behavioral alterations can accelerate or contribute to the extinction process will provide important clues for conservation planning (Anthony and Blumstein 2000). Historically, most behavioral studies have sought study populations that reside in relatively undisturbed habitats to gain insight into evolutionary behaviors. Thus, our collective knowledge on how primates tolerate, persist, and adapt to anthropogenically disturbed habitats is relatively limited. Filling this gap with knowledge of the socioecology of primates in disturbed habitats will provide substantial benefits for conservation managers of those species that inhabit mostly anthropogenically disturbed areas. Additionally, examining behavioral differences between conspecific groups in disturbed and

undisturbed habitats is a valuable comparative method that can provide important tests for behavioral ecology.

7.2 Methods and Analysis

7.2.3 Data Collection

I collected behavioral data on the four study groups detailed above between October 2005 and June 2006. These months captured both the wet and dry seasons in the BMSR region. In general, I cycled through the Reserve and Non-Reserve Groups examining each group for two days in the following repeating order: Green, Teal, Black, Light Blue. Groups proved difficult to locate, particularly those outside the Reserve and this method ensured that I could locate them early on the second day having noted their sleeping site the day before. Observations were made during day-long group follows and rotated through individual group members so as to equalize sample size among individual lemurs. Habituation and distance estimation were secured during the month of September 2005.

All behavioral data were collected on a hand-held, Palm LifeDrive © in Excel. I used BMSR solar panels to recharge the LifeDrive © each afternoon, except when rainy season monsoons prevented the solar panels from being charged. I stored data on rewritable compact discs each week.

In the mornings, as often as possible, I located groups in the sleeping tree or as soon as they began moving. I used 10 - minute focal samples with a one-minute interval to record behavior (Altmann 1974). For each minute I collected the following information: focal individual behavior, location and species of tree involved if individual was arboreal, plant part if feeding, arboreal height (0 if terrestrial), nearest neighbor distance, nearest neighbor location in tree, nearest neighbor height, nearest neighbor behavior. For each 10 minute sample, I also

recorded all occurrences of aggression, inter-troop encounters, GPS location if any movement over 20 m had occurred, general group behavior, group spread, group location in terms of terrestriality or arboreality, and canopy connectedness, group spread (sit close, sitting in contact; close, 2-4 meters; medium, 4-6 meters; far, 6-12 meters; or very far, >12 meters), and if the group was traveling. Additionally, I classified the habitat the lemurs were using in a ranking system to quantify the degree of disturbance. Based on the number of degradation variables present, I gave the habitat (area within 50 m) a number 1-5 depending on the number of the following variables present: evidence of tree cutting, presence of livestock feces, grazing, roads, crops, severe deforestation. These group variables were recorded according to the majority of individuals' behavior, location, etc. These data allowed me to calculate group behaviors and compare between study groups, Reserve vs. Non-Reserve using the number of intervals the particular behavior, location, habitat classification, etc.

7.2.4 Data Analysis

Total sample size on which the analyses are based is almost 300 group follow days which encompass almost 800 hours of contact time. For all analyses involving overall behavior, the full dataset was used. Any grossly incomplete days were excluded so as not to bias the results towards activities that might tend to occur during the period observed.

I investigated differences among groups (all four study groups and Reserve versus Non-Reserve Groups) using Kruskal-Wallis One-Way ANOVAs, using daily rates as variates. In some instances, the rates of observed behaviors were so low that I will only present descriptive analyses to illustrate rates of occurrences between groups.

7.3 Intragroup Spacing

7.3.1 Nearest Neighbor Distances

Overall, ring-tailed lemurs at BMSR spent most of their time within 2-4 meters of their nearest neighbor (Figure 7.1). When all behavioral categories are considered, Reserve Groups are more likely to have shorter nearest neighbor distances (Figure 7.2a, Table 7.1). In fact, focal animals in Reserve Groups are twice as likely to have a nearest neighbor sitting in close contact. Similarly, the likelihood of having no nearest neighbor within 12 m in Non-Reserve Groups is almost four times as high (Figure 7.2b, Table 7.1). Clearly, individuals in Non-Reserve Groups spend more of their time farther from their nearest neighbor. These results are consistent with an increased amount of grooming behavior in Reserve Groups that will be discussed later in this Chapter. Other primate species inhabiting disparate habitats have also been shown to have larger nearest neighbor distances and this is consistent with a higher dietary diversity, more dispersed resources, and food types that have smaller patches. Smaller patches require further spacing in order to avoid feeding conflict (Anthony and Blumstein 2000, Irwin 2006, Isbell and Young 1993).

Table 7.1 Percent of observations that individuals in each group were found in each category of proximity.

	Very Close (sitting in contact)	Close (2-4 meters)	Medium (4-6 meters)	Far (6-12 meters)	Very Far (>12 meters).
Black	5.4%	35.0%	44.4%	14.8%	0.5%
Light Blue	5.7%	43.1%	38.4%	12.7%	0.2%
Green	13.9%	48.5%	32.5%	5.0%	0.1%
Teal	15.9%	53.8%	27.4%	2.8%	0.0%
Non-Reserve	5.5%	38.9%	41.5%	13.8%	0.3%
Reserve	14.7%	50.7%	30.4%	4.1%	0.1%
Total	9.6%	44.2%	36.5%	9.5%	0.2%

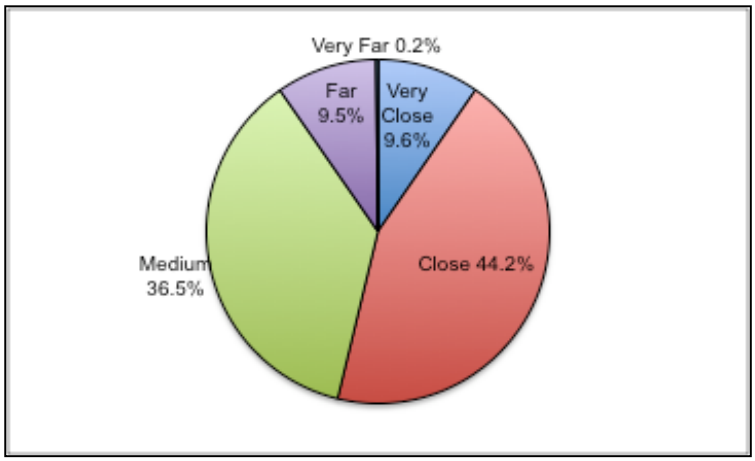


Figure 7.1 Overall Nearest Neighbor distance for all study groups.

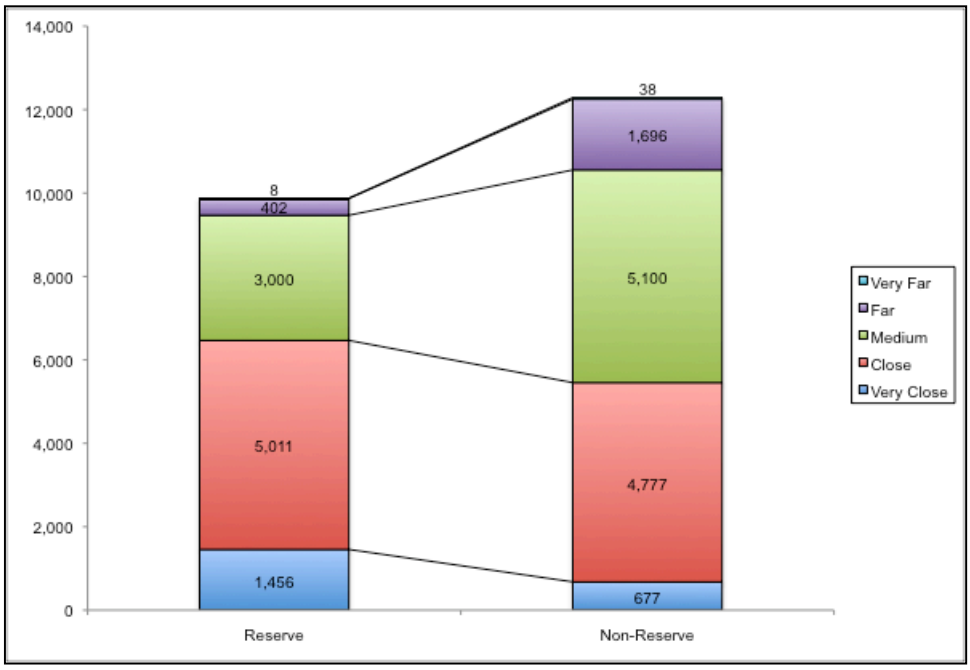


Figure 7.2a Number of instances of nearest neighbor distance categories for Reserve and Non-Reserve Groups. Y-axis indicates number of instances that individuals were found in the coded category of proximity.

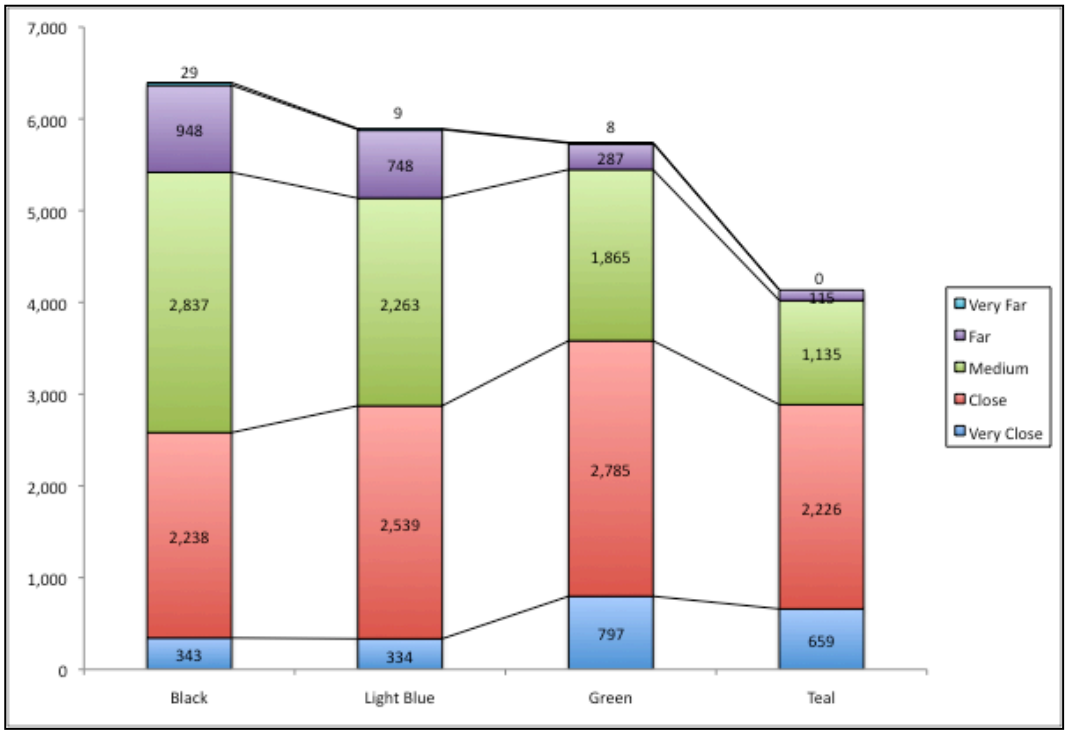


Figure 7.2b Nearest neighbor distances for all four study groups.

7.3.2 Group Cohesion

Group cohesion data were recorded when observing the entire groups' overall dispersion, as opposed to nearest neighbor distance for the focal individual. Overall, groups tend to spend the majority of their time within 2-4 meters of another individual (Figure 7.3a, Table 7.2). Between sites, there are differences in how often the group is relatively closer together and spread farther apart (Figure 7.3b, Table 7.2). Specifically, Non-Reserve Groups tend to spend significantly more time with a larger group spread than Reserve Groups (Table 7.3; Figure 7.4). Within site differences are apparent between Green and Teal Groups where Teal was more likely to have individuals closer together (Figures 7.3c, 7.5). This, however, could be partially contributed to the small group size in Teal after several of the more peripheral males emigrated to other groups.

Table 7.2 Percent of observations that groups spent in 'group spread' proximity categories.

	One	Two	Three	Four	Five
Black	3.7%	23.0%	31.7%	34.2%	7.4%
Light Blue	0.7%	19.4%	38.6%	37.1%	4.2%
Green	11.4%	62.0%	23.0%	3.0%	0.5%
Teal	17.4%	60.9%	15.5%	5.4%	0.7%
Non-Reserve	2.3%	21.3%	35.0%	35.6%	5.8%
Reserve	13.9%	61.6%	19.8%	4.0%	0.6%
Total	7.5%	39.3%	28.2%	21.5%	3.5%

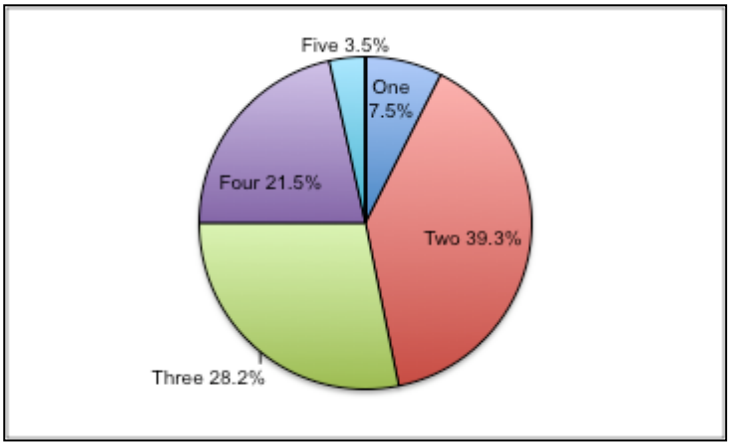


Figure 7.3a Overall time spent in group proximity categories (1= closest, 5=very far).

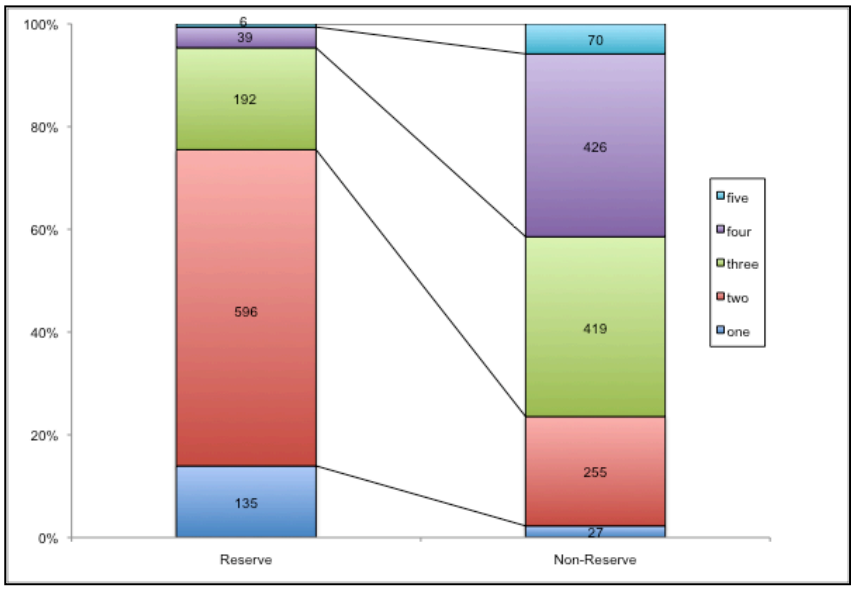


Figure 7.3b Time spent in group proximity categories in Reserve versus Non-Reserve Groups (1= closest, 5=very far).

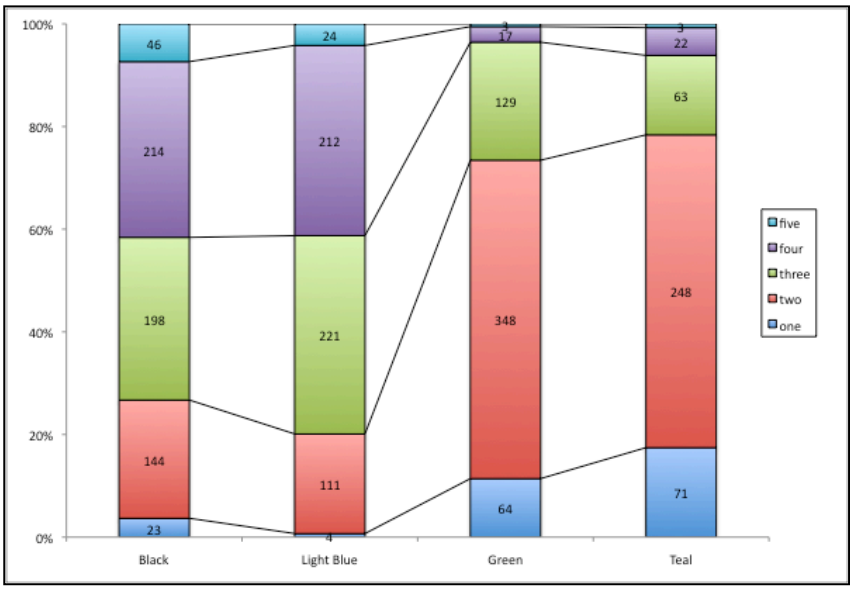


Figure 7.3c Time spent in group proximity categories in all four study Groups (1= closest, 5=very far

Table 7.3 Results of Kruskal Wallis One-Way ANOVAs of median group proximity data comparing the median group spread of each group of all categories.

Comparison of median time spent in all proximity categories in all four study groups	**Value of** Kruskal-Wallis **Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	273.376	0.0001	Y	Y
Black vs. Light Blue	0.740	0.3897	N	N
Black vs. Teal	249.150	0.0001	Y	Y
Green vs. Light Blue	338.589	0.0001	Y	Y
Green vs. Teal	4.472	0.0345	N	Y
Light Blue vs. Teal	302.952	0.0001	Y	Y
Comparison of time spent in proximity categories in Reserve versus Non-Reserve Groups	**Value of** Kruskal-Wallis **Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve versus Non-Reserve	580.568	0.0001	Y	Y

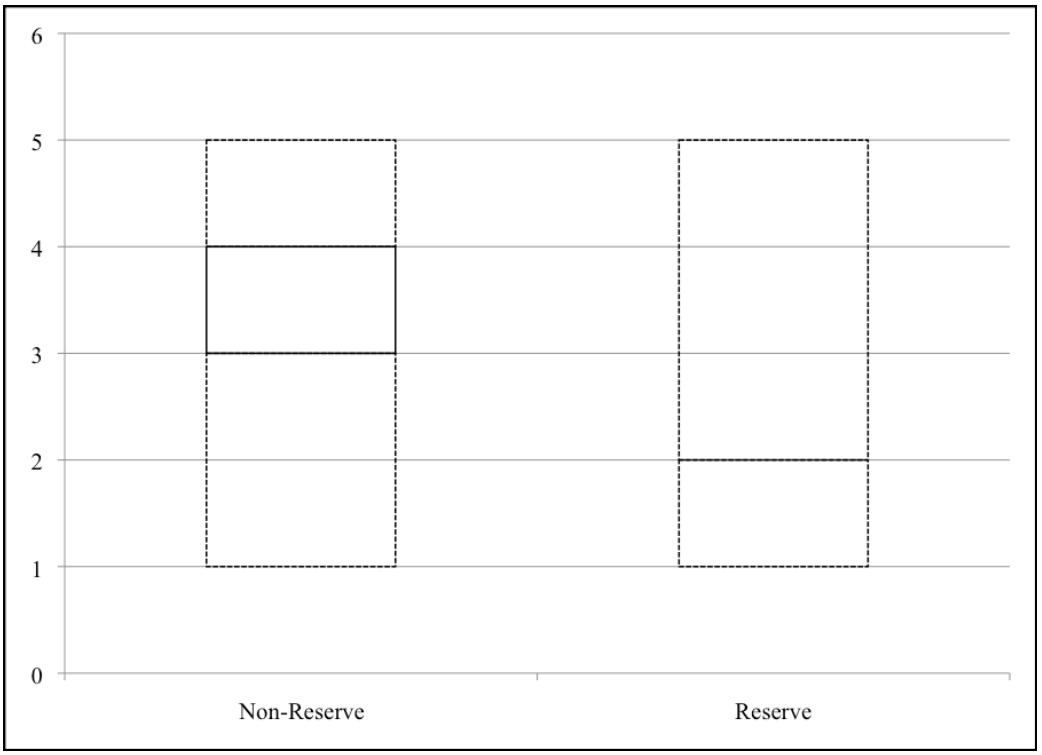


Figure 7.4 Boxplot of Non-Reserve versus Reserve Group proximity data comparing medians.

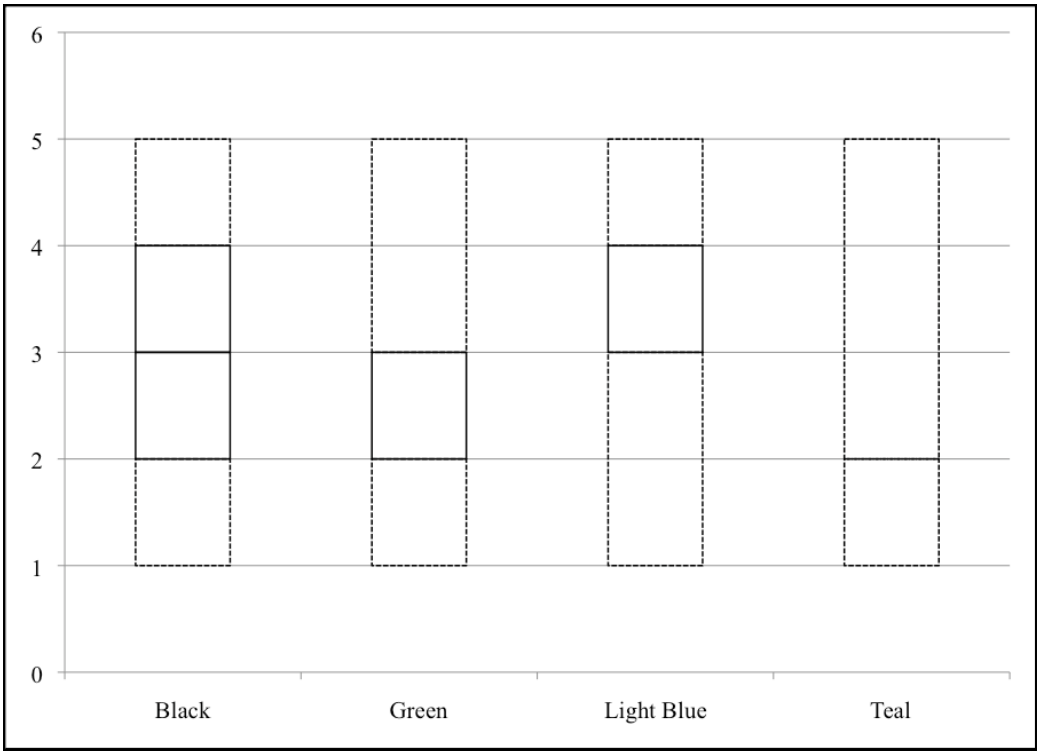


Figure 7.5 Boxplot of each groups' group proximity data comparing medians.

7.4 Affiliative Behaviors

7.4.1 Grooming

Grooming is an activity that often occurs at sleep sites, both in the evening and early morning before a group begins the formal active period of the day. Because of this timing, it is difficult to accurately quantify the total time spent engaged in grooming because grooming occurs when the group is not being observed. Therefore, the absolute time that I have recorded may be an underestimation, as my arrival to the sleep tree in the morning depends on the time that I find the group. Relative measures, however, between the groups are accurate representations of grooming incidence during the active period of the day. The following comparisons, therefore, are measures of the percentage of an animal's active time that was devoted to grooming.

No significant differences were found in quantitative analyses, but there were apparent patterns of grooming differences among the study groups. Inside the Reserve, there were differences in the amount of time individuals spent grooming within Reserve Groups. Specifically, Green Group, possibly due to its long matrilineal history, devoted the greatest amount of time during their active period to grooming (Figure 7.6). Among Reserve Groups, Teal had a lower amount of time devoted to grooming (Figure 7.6). Non-Reserve Groups also had lower rates of grooming and very little within site difference in grooming (Figures 7.6, 7.7). There were no significant differences among Reserve and Non-Reserve Groups because the medians of the groups were not different (Table 7.4).

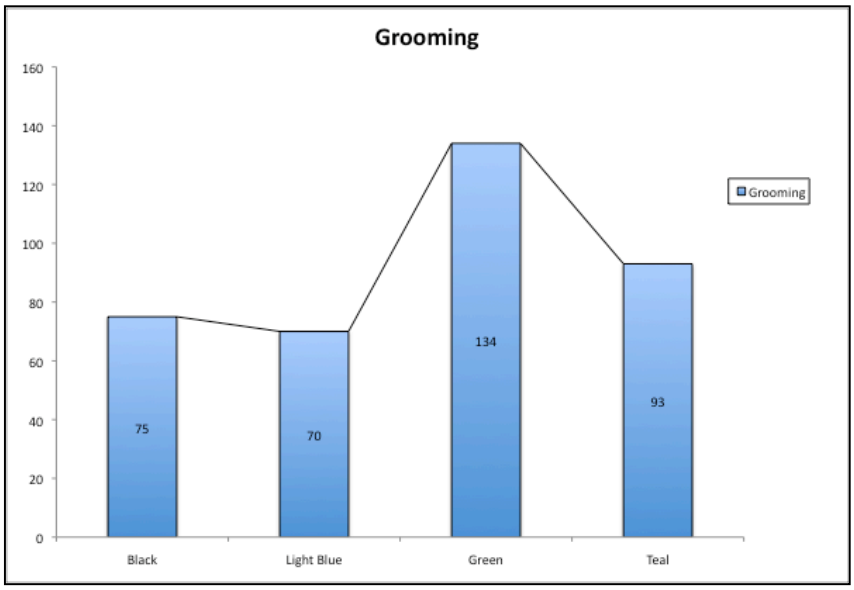


Figure 7.6 Total counts of grooming incidents among all four study groups.

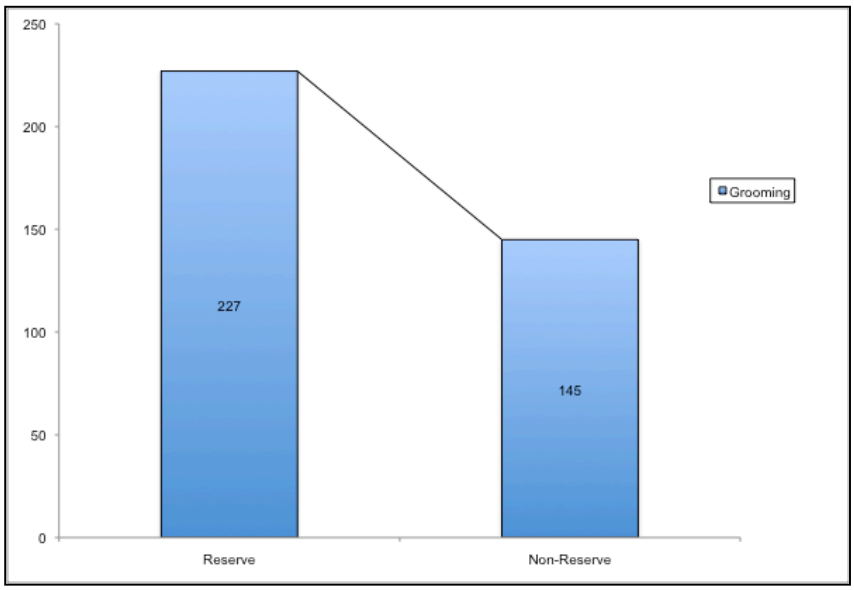


Figure 7.7 Total counts of grooming incidents among Reserve and Non-Reserve Groups.

Table 7.4 Kruskal-Wallis results from comparing median time devoted to grooming among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of time devoted to grooming among all four study groups	**Value of** Kruskal-Wallis **Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	0.533	0.4654	N	N
Black vs. Light Blue	0.318	0.5731	N	N
Black vs. Teal	0.136	0.7123	N	N
Green vs. Light Blue	0.082	0.7740	N	N
Green vs. Teal	0.041	0.8403	N	N
Light Blue vs. Teal	0.028	0.8663	N	N
Comparison of time devoted to grooming among Reserve and Non-Reserve Groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve vs. Non-Reserve	0.197	0.6574	N	N

7.4.2 Playing

Overall, I observed very little play behavior during the study period. Because of this I will discuss this variable descriptively. Overall, immatures and young adults tended to spend the most amount of their active period in play. Inside the Reserve, there were two juveniles in Green Group until the Trois Fromage Group left, taking the younger one with them. Among Non-Reserve Groups, Light Blue Group had several younger adult males that engaged in play. Black Group, like Green Group after its fission, had only one younger male. Teal Group's only juvenile died early in the study period. When there were two infants present in a group (only in Green and Black Groups for a short period) those individuals engaged in play. Considering these factors, it is not surprising, that there are no significant differences among groups when playing

is analyzed, although Non-Reserve Groups' level of play approach significance at the 10% significance level (Table 7.5). The Kruskal Wallis test compares the medians across groups, and, in this case, they are the same despite any differences in maxima/minima or total instances. Elevated levels of play in Non-Reserve Groups (Figure 7.8) are mostly due to the larger number of young adult males in Light Blue Group that would occasionally engage in play behavior (Figure 7.9). Play behaviors were more likely to occur in months when more food is available (November through March). This may be attributed to play being a more energetically demanding activity, and colder temperatures and slightly shorter day lengths during the drier, less resource-abundant months. Notably, groups that are in more disturbed habitats, traveling more during the day, also show elevated levels of play. Additionally, while Non-Reserve Groups show lower levels of grooming, the fact that there are higher levels of play suggests that grooming and play behavior serve different social purposes for different age and sex classes.

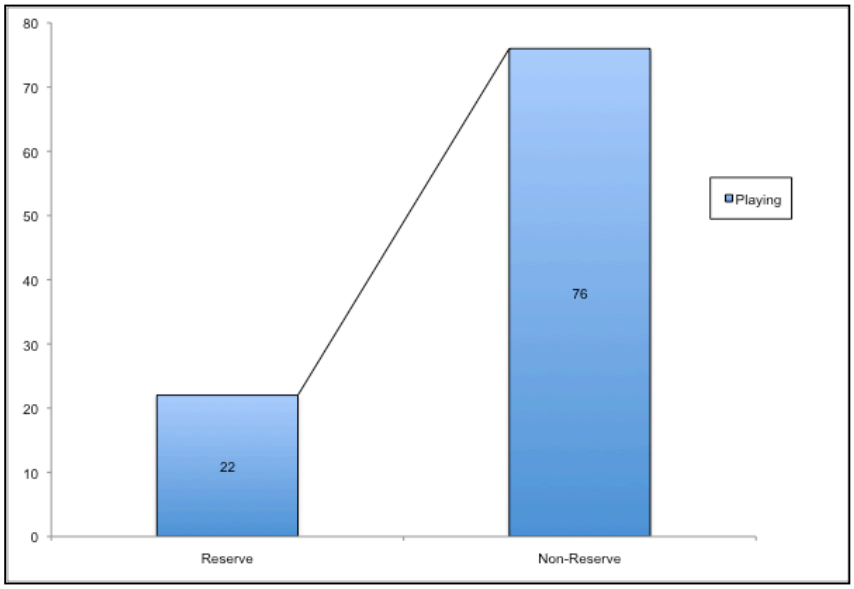


Figure 7.8 Observed incidences of play in Reserve and Non-Reserve Groups.

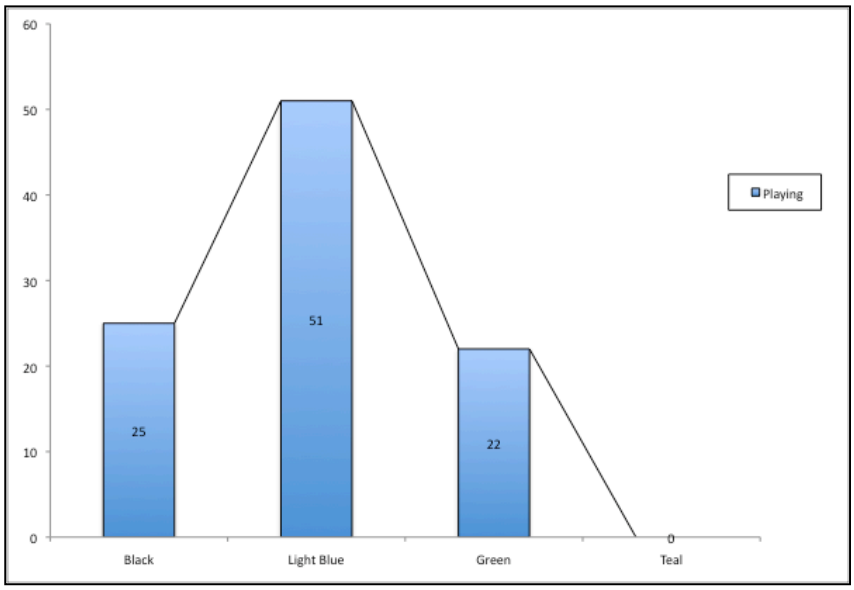


Figure 7.9 Observed instances of play in all four study groups.

Table 7.5 Kruskal-Wallis results for comparisons of median play observations among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of play observations among all four study groups	Value of Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	0.664	0.4151	N	N
Black vs. Light Blue	0.274	0.6004	N	N
Black vs. Teal	1.224	0.2686	N	N
Green vs. Light Blue	1.670	0.1962	N	N
Green vs. Teal	0.117	0.7319	N	N
Light Blue vs. Teal	2.295	0.1298	N	N

7.5 Aggressive Behaviors

7.5.1 Rates of Aggression

Aggressive behaviors including displacements, chases, cuffs, biting, grabbing, and lunging, occurred about 5% of the observation time in and around BMSR (Figure 7.10a). While within-site differences in observations of aggression were non-existent, there were significant

differences between the Reserve and Non-Reserve Groups (Table 7.6; Figures 7.10a, b; 7.11a, b). Specifically, Black and Light Blue Groups were observed engaging in aggressive behavior at a significantly higher rate than both Teal and Green Groups (Figure 7.10c). Adults experienced the vast majority of aggression and very little seasonal variation was evident. These bouts of aggression included both intra- and intergroup activities. It is surprising that groups in more disturbed areas engaged in energetically demanding activities because dietary differences, increased daily path lengths, and elevated rates of traveling might have made these activities more taxing. Interestingly, aggression rates are higher for the Non-Reserve Groups (Black and Light Blue) that tend to have a larger group spread and larger nearest neighbor distances. However, there may be a price for this larger spread: being farther apart reduces effectiveness of vigilance for predators. It is possible that Non-Reserve Groups have a higher propensity for aggression due to tensions stimulated by predators and human presence. The overall heightened vigilance may incur higher potential for aggression. Higher stress levels have been shown to result in higher rates of aggression in sifaka (Irwin 2006). Moreover, if food resources are reduced or of lesser quality, individuals may demonstrate higher rates of aggression to defend resources. In the vast majority of cases, I observed a submissive signal given by the recipient of aggression (usually this was a 'chatter' vocalization, grooming the aggressor, or spatially avoiding the aggressor). As such, it was evident that the relationships among individuals in a group were relatively stable and aggression predominantly reinforced well-established dominance relationships.

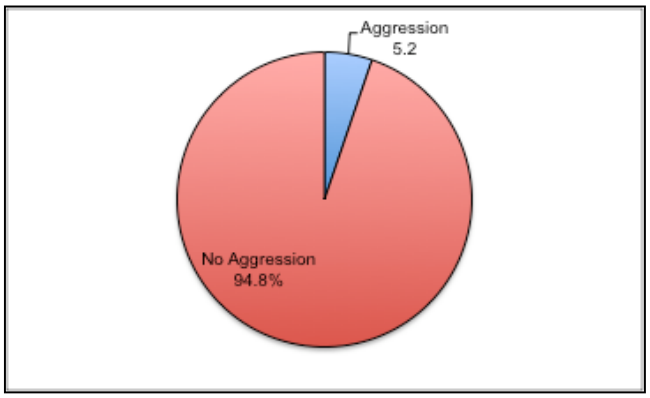


Figure 7.10a Overall incidence of aggression among all four study groups.

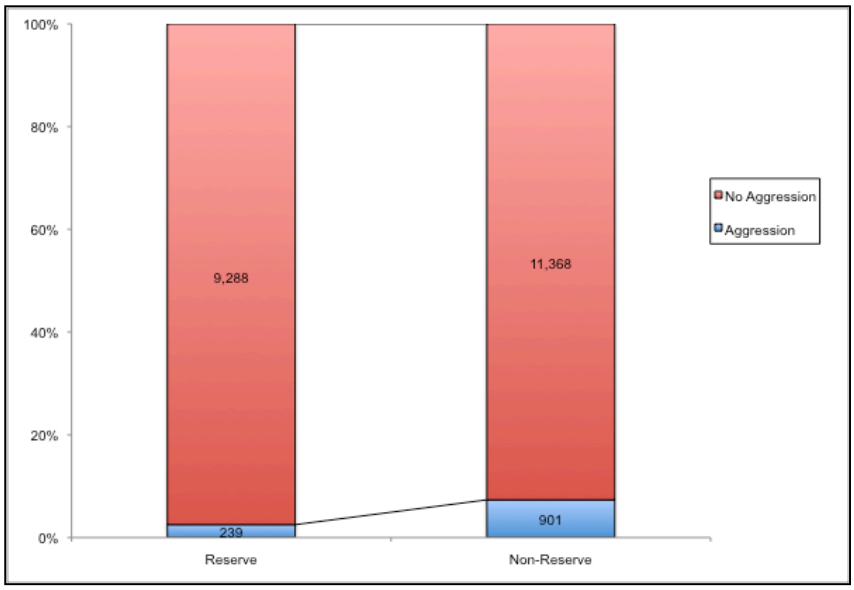


Figure 7.10b Observations of aggression in Reserve and Non-Reserve Groups.

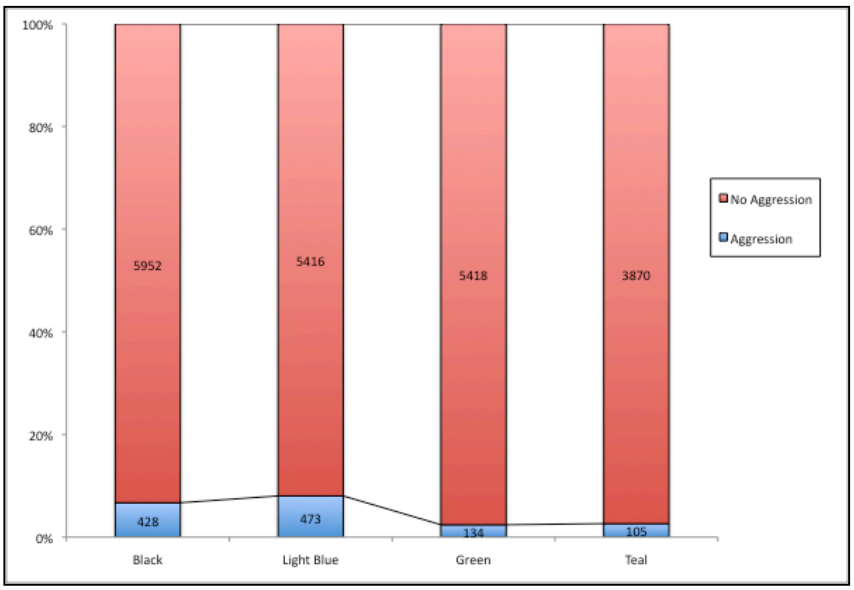


Figure 7.10c Observations of aggression in all four study groups**.**

Table 7.6 Results from Kruskal-Wallis comparisons of median observations of aggression among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of observations of aggression among all four study groups	**Value of** Kruskal-Wallis **Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	6.447	0.0111	N	Y
Black vs. Light Blue	0.791	0.3739	N	N
Black vs. Teal	5.041	0.0248	N	Y
Green vs. Light Blue	10.533	0.0012	Y	Y
Green vs. Teal	0.049	0.8246	N	N
Light Blue vs. Teal	8.417	0.0037	Y	Y
Comparison of observations of aggression among all Reserve and Non-Reserve Groups	**Value of** Kruskal-Wallis **Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Reserve versus Non-Reserve	15.341	0.001	Y	Y

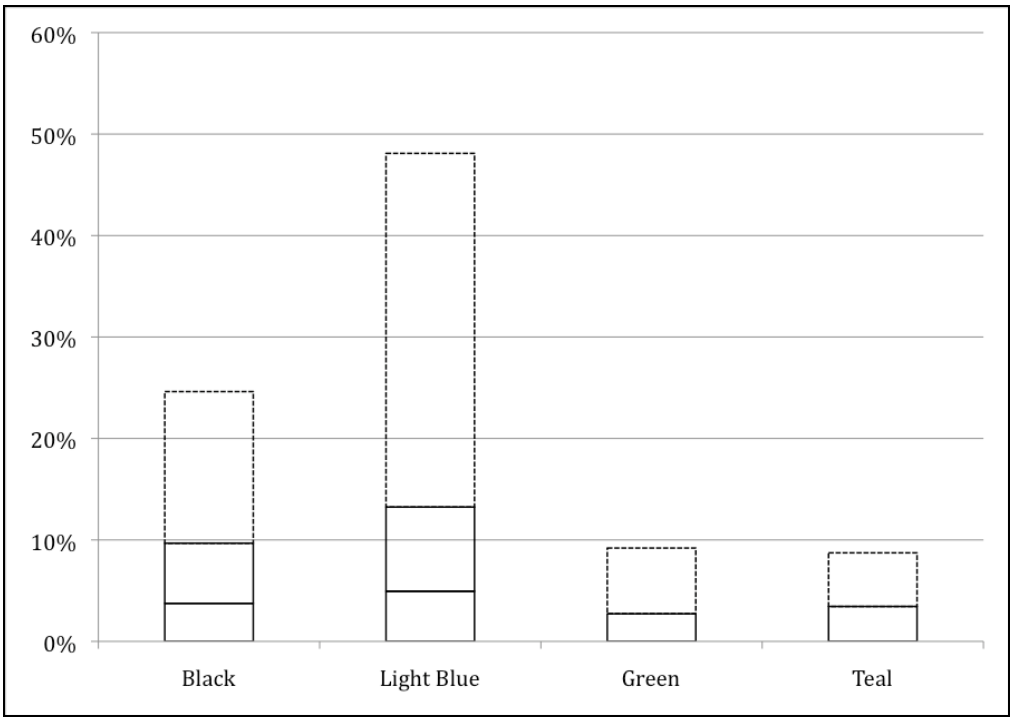


Figure 7.11a Boxplot of aggressive behavior observations among all four study groups.

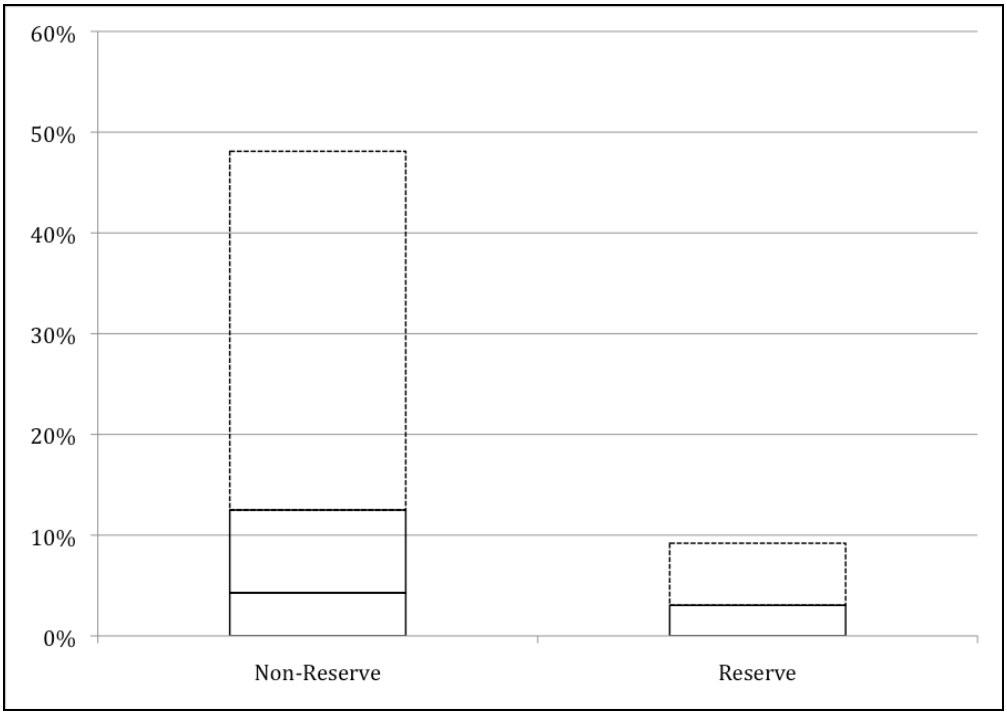


Figure 7.11b Boxplot of aggressive behavior observations among Reserve and Non-Reserve Groups.

7.5.2 Context of Aggression

About half of the aggressive acts occurred during feeding contexts. Dominant animals typically directed aggression towards lower-ranking individuals as they arrived at food resources, thereby displacing the lower-ranking individual (Table 7.7). Or, the subordinate individual left prior to the arrival of the dominant individual as the subordinate saw them approaching. There were no clear habitat-related differences in the percentage of aggressive behaviors associated with feeding behavior (Black 56%; Light Blue 50%; Green: 52%; Teal 42%). It is possible that Non-Reserve Groups mitigated feeding related aggression with increased spacing to avoid food-related conflict as much as possible. Some habitat-related differences in the percentage of aggression occurred when individuals were in close proximity to each other and in close proximity to other groups (Table 7.7). None of the group-level comparisons of aggression and intergroup encounters, feeding, or proximity are statistically significant.

Table 7.7 Context of instances of aggression for each group.

Group	Close Proximity	Intergroup encounter	Feeding	Other
Light Blue	16%	33%	50%	8%
Black	12%	22%	56%	5%
Green	8%	16%	52%	24%
Teal	21%	15%	42%	22%

7.6 Scentmarking

Interestingly, scentmarking accounted for 1.0% of all recorded behaviors. The types of scentmarks employed differed between sexes. Females used only anogenital gland marking, sometimes accompanied by urination. Males used carpal marking frequently – rubbing carpal spurs on sternal glands and then gouging small diameter (1-3 cm) trees with their carpal spurs. Results indicate that there were significant between site differences, while within site

scentmarking observations were quite similar (Table 7.8; Figures 7.12, 7.13). Specifically, both Black and Light Blue Groups scentmarked more than either Green or Teal, although this is not statistically significant when comparing Green with Light Blue Group. Black Group (with a range sandwiched between the Reserve, the research camp, and the river) had the highest number of scentmarking behaviors. Interestingly, they regularly came into contact with another collared group (Orange) in the research camp area. This is also notable in light of their smaller home ranges and longer daily path length: these variables may have heightened the occurrence of scentmarking if they were coming into contact with other groups, or other group's scentmarks, more frequently. The elevated level of scentmarking activity among Non-Reserve Groups may reflect an increased level of intergroup communication and possibility of attracting mating partners, or warding off potential incursions from other groups.

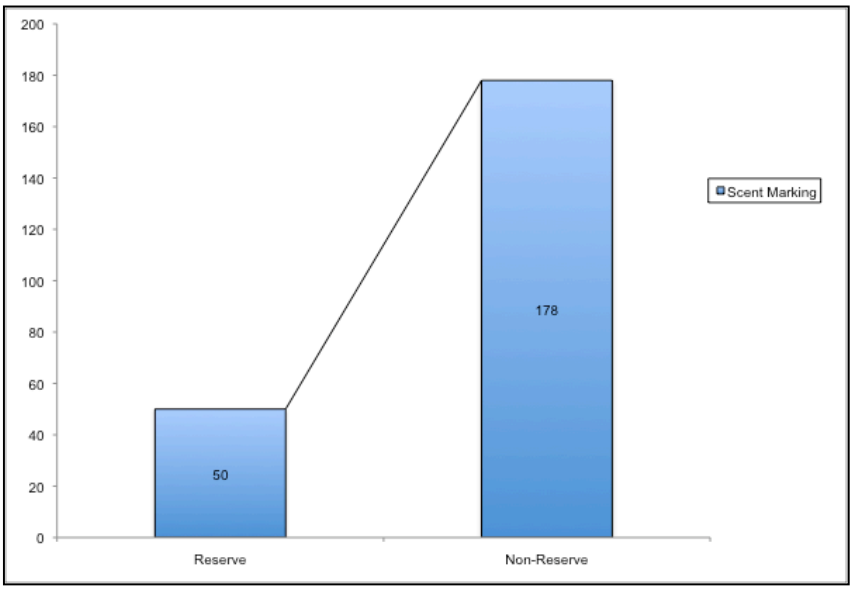


Figure 7.12 Amount of time devoted to scentmarking and number of observations in Reserve and Non-Reserve Groups.

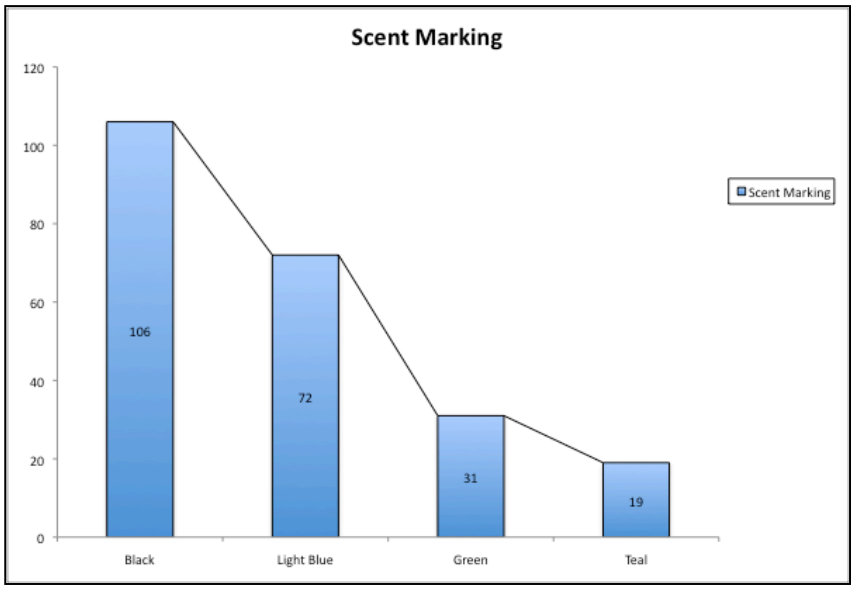


Figure 7.13 Amount of time devoted to scentmarking and number of observations in all four study groups.

Table 7.8 Kruskal-Wallis results comparing median scentmarking observations among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of scentmarking observations among all four study groups	**Value of Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	8.895	0.0029	Y	Y
Black vs. Light Blue	2.085	0.1488	N	N
Black vs. Teal	14.412	0.0001	Y	Y
Green vs. Light Blue	2.927	0.0871	N	N
Green vs. Teal	2.648	0.1037	N	N
Light Blue vs. Teal	9.666	0.0019	Y	Y

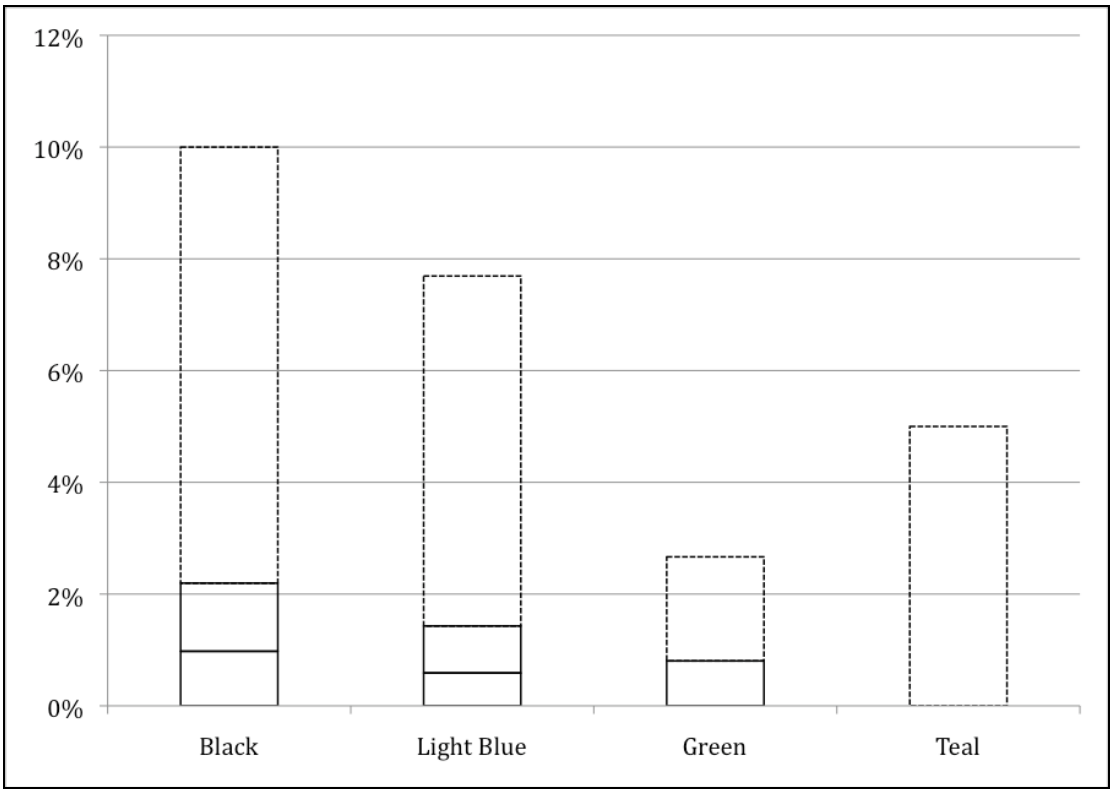


Figure 7.14 Boxplot of scentmarking behavior observations among all four study groups.

7.7 Intergroup Encounters

The number of intergroup encounters was difficult to assess quantitatively, due to the low numbers of observations throughout the study period. Overall, the number of intergroup encounters were relatively similar among Reserve and Non-Reserve Groups (Figure 7.15). Green Group had slightly more intergroup encounters. This may be a result of this group having more overlap of core areas with neighboring groups, and denser populations of lemur groups (not individuals). Historically, groups (such as Green) that border the Sakamena have fought to defend particularly rich resources. Green Group regularly came into contact with Red, Lavender, and Teal Groups. Outside the Reserve, Black Group overlapped with both Orange Group where their ranges met, and Light Blue Group. Light Blue Group came into contact with an uncollared

group to the south and Black Group. Reserve Groups may be more settled, or secure, in their traditional home ranges. On the other hand, with recent anthropogenic disturbance and reduction of traditional/historical ranges, even with the absence of significantly higher intergroup encounters, groups may be traveling more as they establish territorial boundaries in areas with higher rates of human traffic, grazing activity, and agricultural activities, and recently acquired territorial boundaries.

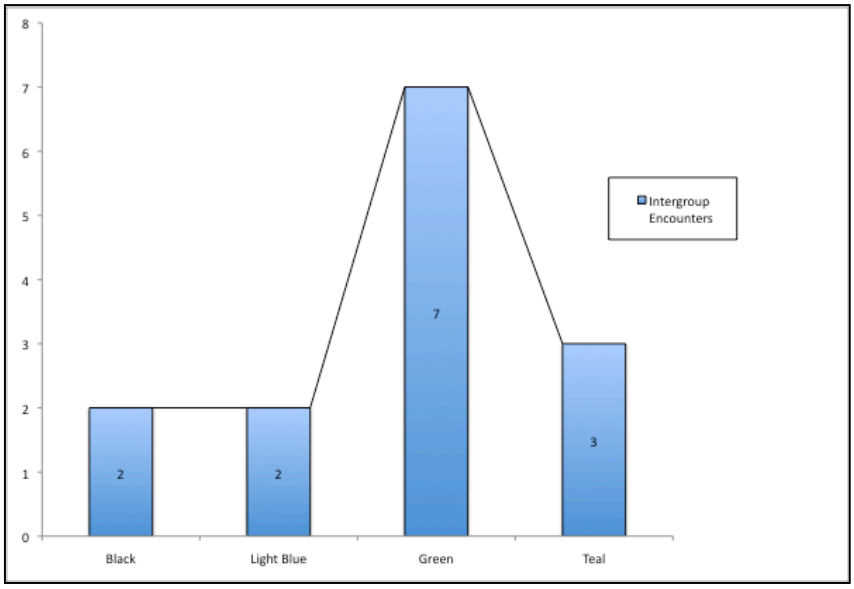


Figure 7.15 Number of observed intergroup encounters for each study group.

7.8 Vocalizations

Overall, groups outside the Reserve tend to communicate more than groups inside the Reserve (Figure 7.17, Table 7.9). These observations included contact calls, alarm calls, and various other vocalizations. There were relatively few observations of vocalizations throughout the study period, but despite this, there is a clear difference. These data refer primarily to alarm calls. For instance, Black Group vocalized significantly more than both Green and Teal (Table

7.10). These calls can mostly be attributed to a heightened number of alarm calls (16 for Light Blue, 12 for Black). This might also be related to the lack of visual contact between neighboring groups, and an increased reliance on vocal and scentmarking communication to clearly establish boundaries. Furthermore, in more anthropogenically disturbed habitats, alarm calls can help group members avoid potential predator encounters. As will be discussed in the next chapter, Black and Light Blue Groups both experience elevated exposure to predators.

Table 7.9 Number of (primarily alarm calls) vocalizations recorded for each study group.

	Number of Vocalizations
Black	17
Light Blue	19
Green	1
Teal	3
Non-Reserve	36
Reserve	4
Total	40

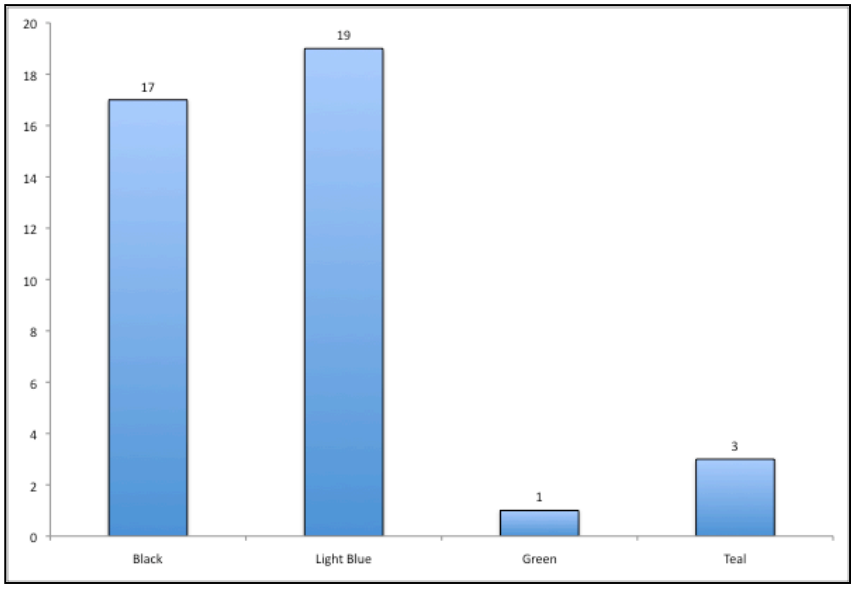


Figure 7.16 Number of vocalizations recorded for each study group.

Table 7.10 Kruskal-Wallis results comparing vocalization observations among all four study groups and Reserve versus Non-Reserve Groups.

Comparison of vocalization observations among all four study groups	Value of Test Statistic	P-Value	Reject H_0 at 1% sig. level?	Reject H_0 at 5% sig. level?
Black vs. Green	4.115	0.0425	N	Y
Black vs. Light Blue	1.351	0.2452	N	N
Black vs. Teal	3.164	0.0453	N	Y
Green vs. Light Blue	4.211	0.0402	N	Y
Green vs. Teal	0.003	0.9558	N	N
Light Blue vs. Teal	4.212	0.0463	N	Y
Comparison of vocalization observations among Reserve and Non-Reserve Groups	Value of Test Statistic	P-Value	Reject H_0 at 1 % sig. level?	Reject H_0 at 5% sig. level?
Reserve vs. Non-Reserve	3.272	0.0505	N	Y

7.9 Vigilance Behavior

As will be discussed in the next chapter, groups outside the Reserve encountered more predators than groups inside the Reserve. It is expected, therefore, that Black and Teal will practice more vigilance because there are more instances of disturbance in their habitat (including humans walking, agricultural activity in fields, domestic animals including zebu, goats, sheep, and dogs) wild cats, and zebu-drawn carts (Table 7.9). Vigilance behaviors include scanning and sentinel behaviors. Indeed, results indicate that Non-Reserve Groups increased vigilance behaviors during the study period (Figure 7.17, 18, 19; Table 7.9, 10). Non-Reserve Groups were significantly more vigilant than Reserve Groups (Table 7.10, Figure 7.18,19).

Vigilance behavior increased in all groups in exposed areas, especially for those that crossed the dry riverbed to access resources in agricultural areas that were nearly devoid of trees. These sought after resources included *Azima tetracantha, Mangifera indica, Tamarindus indica.* The groups that accessed resources across the Sakamena in particular were Black and Light Blue. Over the course of the study period, Black crossed the river 15 times, Light Blue crossed 12, Green crossed six times, and Teal never crossed the river.

Table 7.11 Number of vigilance behaviors in each group and in Reserve vs. Non-Reserve Groups.

	Number of Vigilance Behaviors
Black	27
Light Blue	25
Green	3
Teal	0
Non-Reserve	52
Reserve	3
Total	55

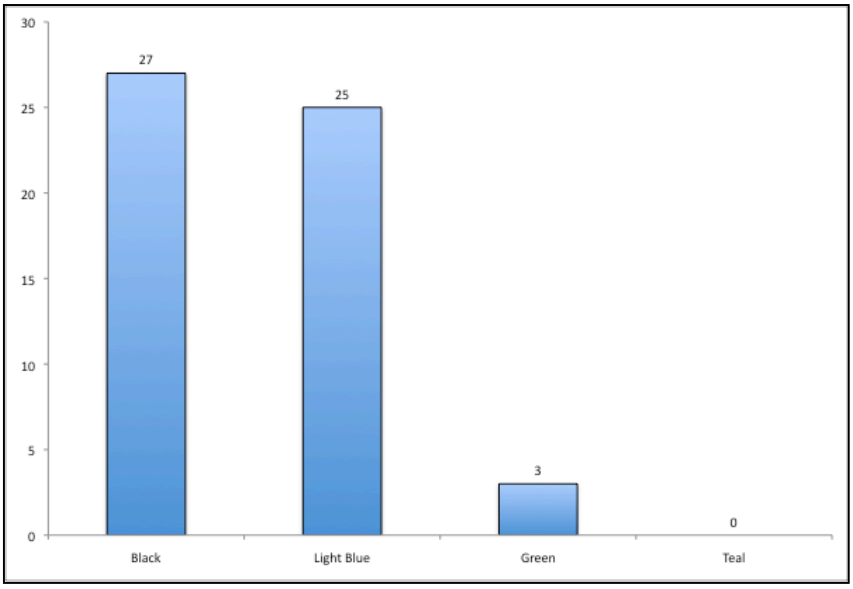


Figure 7.17 Number of vigilance behaviors recorded for each study group.

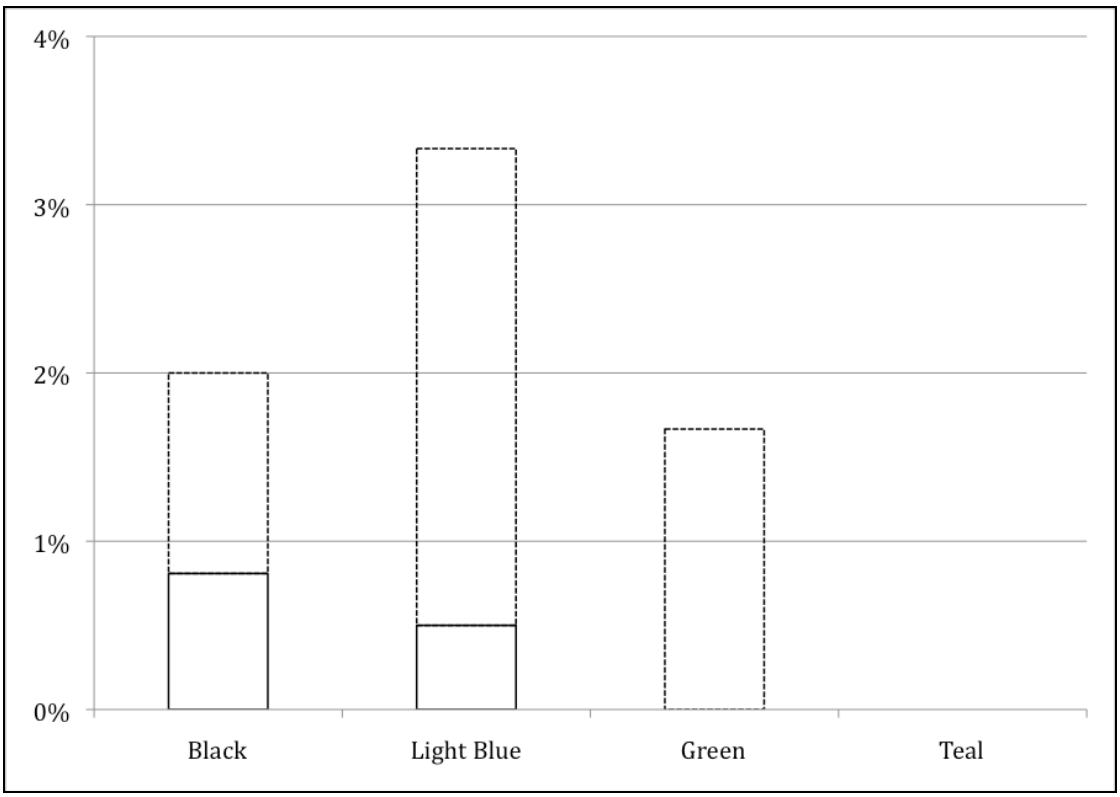


Figure 7.18 Box plot comparing median vigilance instances between all four study groups.

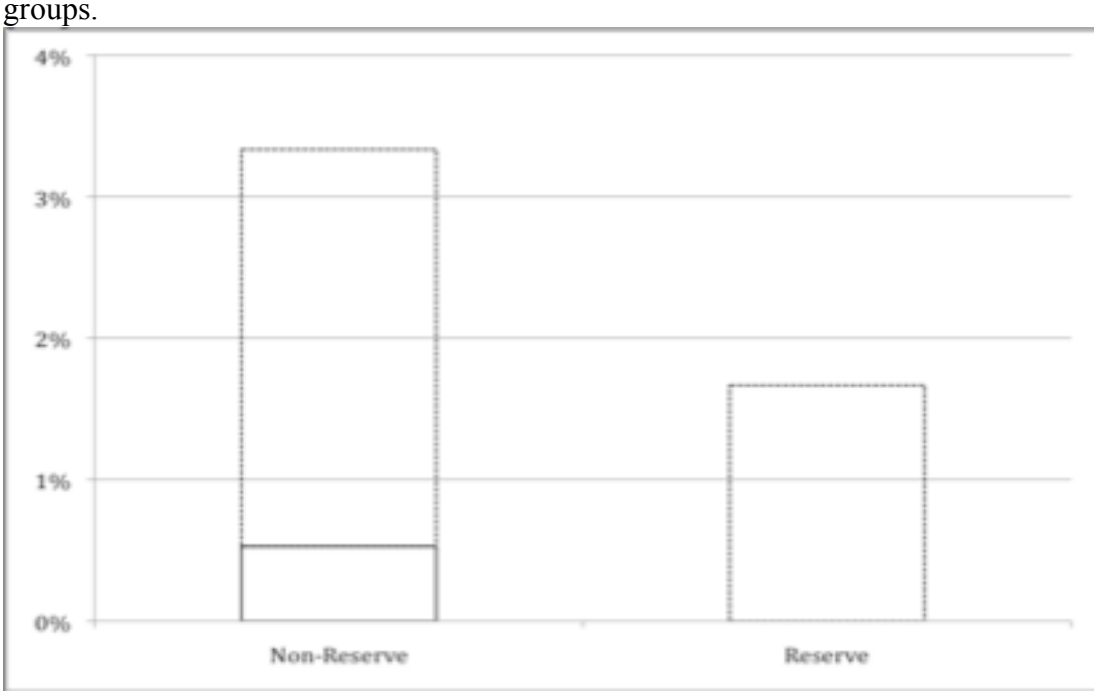


Figure 7.19 Box plot comparing median vigilance instances between all Reserve and Non-Reserve Groups.

Table 7.12 Kruskal-Wallis results comparing median vigilance observations among all four study groups.

Comparison of vigilance behaviors among study groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Black vs. Green	6.110	0.0134	N	Y
Black vs. Light Blue	0.210	0.6471	N	N
Black vs. Teal	7.650	0.0057	Y	Y
Green vs. Light Blue	4.801	0.0284	N	Y
Green vs. Teal	0.264	0.6073	N	N
Light Blue vs. Teal	6.375	0.0116	N	Y
Comparison of vigilance behaviors between Reserve and Non-Reserve Groups	**Value of Kruskal-Wallis Test Statistic**	**P-Value**	**Reject H_0 at 1% sig. level?**	**Reject H_0 at 5% sig. level?**
Vigilance	12.237	0.0005	Y	Y

7.10 Discussion

Anthropogenic habitat disturbance has been shown to influece the diet of the ring-tailed lemur at BMSR. While social organization and patterns of affiliation remain constant in these disturbed habitats, patterns of group cohesion and rates of certain social behaviors and modes of communication differ between protected and unprotected habitats.

Groups in unprotected habitats have greatly reduced group cohesion. This may be related to their more diverse diet in that they focus on fruits from several different types of trees that tend to occur in smaller patches. In contrast, Reserve Groups utilize larger patches of fruit (such as *Tamarindus indica*) and terrestrial herbs. Non-Reserve Groups focus on *Tallinella grevea*, *Grewia leucophylla*, and *Grewia grevei* fruit that tend to be smaller trees and sometimes cannot accommodate more than one individual. This ecological shift may be the catalyst for alterations in other variables of behavior and ecology for these groups.

Consistent with larger nearest neighbor distances and less overall group cohesion, Non-Reserve Groups had lower rates of grooming among individuals. This may be caused by the increase in both feeding and traveling time that was discussed in the previous chapter. Contrary to the reduced time spent in grooming, other affiliative behaviors, such as playing were slightly increased in Non-Reserve Groups. It is possible that the significantly higher number of immature males in Light Blue Group might influence this increase. The participation of individuals inhabiting more disturbed habitats in this energy-intensive activity suggests that their energy levels are not critically constrained so resources are adequate to enable this behavior or that the importance of play in growth and development remains important (Bekoff 1984, Breugeman 1978).

The context of aggression was similar across all sites with about half of all aggressive occurrences associated with feeding. Overall rates of aggression were elevated in Non-Reserve Groups. This was surprising given the overall increase in distance between individuals. Despite the apparent strategy to increase inter-individual distance, resource defense and tensions were still high enough in Non-Reserve Groups to warrant more aggressive behaviors between individuals, this may be related to the recorded increase in aggression during closer proximities of group members and during intergroup encounters. Additionally, it is possible that this increase in aggression was a result of the more stressful habitat requiring more feeding time, more traveling time, and allowing less time for the affiliative behaviors that reinforce and stabilize social relationships in groups.

Rates of scentmarking are elevated in Non-Reserve Groups and this may be primarily related to their smaller home ranges and increased daily path lengths, as has been suggested in other studies (Erhart 2008, Kappeler 1998, Parga 2006). Though they have moderately reduced

intergroup encounters, they may be coming into contact with scentmarks from other groups, hearing vocalizations, and be more stressed to defend the smaller resource base that they utilize more comprehensively than groups inside the Reserve. Non-Reserve Groups were less predictable in their ranging patterns based on their daily path lengths and larger home ranges and core areas. They were more prone to travel quickly to new areas, and therefore came into contact with nearby groups (and their scents) more frequently than the more sedentary Reserve Groups.

Other behaviors were also moderately elevated in Non-Reserve Groups including vocalizations and vigilance behavior. This evidence suggests that there are increased stimuli that were particularly alarming to Non-Reserve Groups that affected the rate of communication among individuals. For example, alarm calls and instances of vigilance were more common outside the Reserve requiring more communication, a heightened sense of vigilance, and a more stressful existence. As Non-Reserve Groups experienced more encounters with predators which periodically resulted in more sustained injuries, these behaviors appear related to the more dangerous nature of Non-Reserve habitats during the study period (see Chapter 8).

While the consequence of any of these behaviors to long-term survival and viability in anthropogenically disturbed habitats is difficult to ascertain, it is relevant to assert that many of these behavioral shifts may represent adaptations to ring-tailed lemurs' altered environments around BMSR. From the results in this chapter, there are several important observations and conclusions that are relevant to the future of this population as a whole.

First, with consistently lower group cohesion, increased group spread, predation risk may be higher for Non-Reserve Groups. In fact, members of these groups do incur more injuries and have a lower survival rate than those groups inside the Reserve during this study. While there were no eye-witness observations of predation made during the study period, there were frequent

observations of predators stalking and chasing lemurs. These theats were primarily by dogs, feral cats, and raptors. Each of these potential predators elicits antipredator responses from ring-tailed lemurs. The largest Malagasy carnivore, the fossa (*Cryptoprocta ferox*) has recently been sighted around BMSR through the use of night cameras (Sauther and Cuozzo, unpublished data). In other parts of Madagascar, fossa predation appears to be more frequent in anthropogenically disturbed forests and fragments (Goodman 2003, Iwrin and Raharison in prep, Patel 2005). Lemurs in more disturbed areas may be more vulnerable to predation due to their larger group spread. Higher rates of vigilance behavior may be able to alleviate some of this predation pressure. However, increased time spent in vigilance reduces time available for feeding and affiliative social behaviors. During predator sightings in the study period, lemurs immediately retreated to the upper canopy of the forest, ran away from the predator, and remained quiet and inactive for the majority of the morning or the afternoon of the event. In effect, it would disrupt their daily path and daily activities of foraging and feeding. Predators could pose a clear threat to the viability of populations outside the Reserve as groups are consistently more spread out. The threat is particularly grave to immature lemurs when foraging alone.

There is indirect evidence that several behavioral shifts may indicate higher energy expenditure among individuals in Non-Reserve Groups. The decreased engagement in grooming (a lower energy behavior) and resting, but increased scentmarking and aggression, coupled with the increase in daily path length strongly suggests that Non-Reserve Groups are expending more energy that Reserve Groups on a daily basis. Therefore, to be in energy balance and maintain a viable population, these individuals probably require a higher energy intake than groups inside the Reserve. Non-Reserve Groups appear to have a different feeding strategy focusing on a wider variety of food species, and it will be necessary to examine the chemical composition of foods in

Reserve and Non-Reserve sites to determine the direct impact of dietary differences between these sites.

Finally, a more general result that may have dire consequences is the lower amount of intergroup encounters in Non-Reserve Groups. While Non-Reserve Groups did exhibit more scentmarking, possibly due to the longer daily path lengths, they also encountered neighboring groups less than groups inside the Reserve. Moreover, groups inside the Reserve were observed to disperse, fractionate, and have more dynamic group encounters than groups outside the Reserve. Groups outside the Reserve were observed to have fewer direct encounters with other groups. More than likely, subadult males use their knowledge of the social landscape to make choices about where and when to disperse (Irwin 2006). If subadults lack this information about neighboring groups, encounter more challenging and exposed landscapes between forest habitats, or suffer higher mortality or unsuccessful dispersals between groups, then this could lead to altered demography or genetic structure in populations. This potential demographic threat is a larger picture, and longer term, consequence of observations made during this study period. The current presence of lemurs in these degraded landscapes, especially with longer life spans, may be masking a longer-term problem of unviable populations. Tracking these groups, both inside and outside the Reserve, will be vital to understanding the effects of habitat disturbance.

While several of the assertions here may be generalizations based on indirect observations from a 9-month study, many of these slight behavioral shifts are most likely the result of dietary shifts and spatial patterns of food resources. Species in more degraded areas will most likely feed on fallback foods that are dispersed differently in space. Comprehensive and species-specific study will be necessary to fully understand and predict how social behavior changes in altered habitats.

It is important to recognize the multitude of potentially cascading effects of anthropogenically altered habitats surveyed in this study. *Lemur catta* appears to be ecologically compatible with altered habitats outside of the small protected Reserve, but has made a series of changes in activity budget, ranging patterns, and behaviors that appear to be maintaining viable groups currently. These behavioral changes, or compromises, have the potential to affect long-term viability through their combined effects on survivorship, reproduction, successful dispersal, and stress, which may also affect prevalence of disease, malnutrition, and predation vulnerability.

CHAPTER 8

UNDERSTANDING THE POWER OF PROXIMATE MECHANISMS: PATTERNS OF RING-TAILED LEMUR (*LEMUR CATTA*) SURVIVAL AT BEZA MAHAFALY SPECIAL RESERVE

8.1 Introduction

Long-term studies are critical for determining the dynamics of demography in wild primates (Crockett and Eisenberg 1986, Fleagle et al. 1999, Rudran and Fernandez-Duque 2003, Strier and Boubli 2006, Sussman 1991). Indeed, as some researchers have noted, "until we know the effect of population fluctuations and understand the processes driving these changes, we will not be able to fully explain the observed species-specific life-history strategy as an adaptive response to the environment" (Rudran and Fernandez-Duque 2003: 935). Long-term research produces essential information from primate populations around the world and provides the basis for behavioral theory and applied methodology. However, the mechanisms behind these demographic changes are complicated and are often attributed to unseen, assumed and postulated macro-mechanisms and stochastic events. One study, for example, attributed a howler population decline to disease, but also noted that recently regenerated forest food shortages and periods of drought may also have contributed to this decline (Rudran and Fernandez-Duque 2003).

Furthermore, most long-term demographic studies census groups once per year, possibly missing important events that are shaping the census results (Chapman and Balcomb 1998). To clearly understand critical mechanisms that may drive primate survival from year to year, it is imperative to record the day-to-day challenging events that cause populations to fluctuate. These proximate events are key to understanding population fluctuations. Here I present an examination of a primate population's struggles through a micro lens – examining the daily

challenges that young ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Special Reserve in southwestern Madagascar face on their way to adulthood. Survival is obviously key for young primates and the challenges to infant juvenile survival are often the mechanisms that drive population fluctuations over several generations.

8.1.1 Objectives

This chapter will offer a preliminary report on the effects of anthropogenic habitat disturbance on several demographic points for *L. catta* in and around Beza Mahafaly Special Reserve. Specifically, I address the following questions:

1.) What are the environmental factors that change population parameters?

2.) What are some of the predictable versus unpredictable causes of survival for young lemurs?

3.) In what ways does anthropogenic habitat disturbance affect birth rates and patterns of mortality?

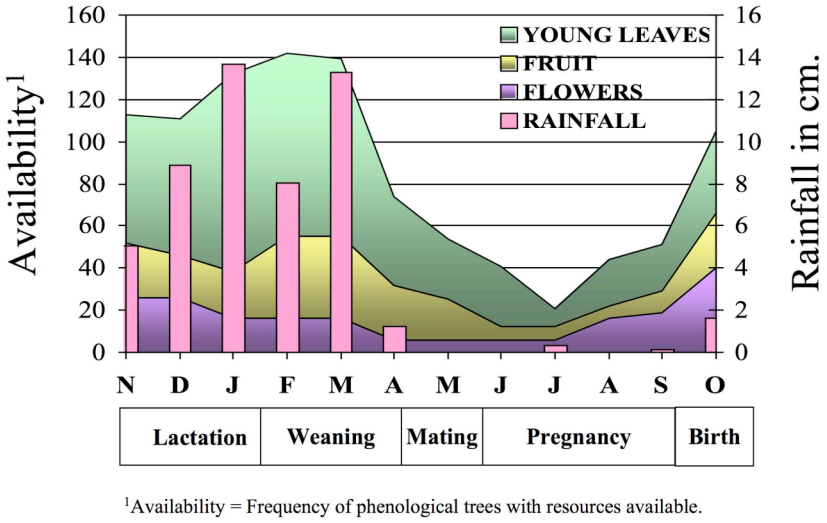
The answers to these questions will contribute an initial understanding of *L. catta* tolerance and persistence in the face of challenging habitat changes. With this knowledge, conservation managers and policy makers will be better equipped to make sound decisions and priorities for the persistence of this species. This study will also contribute to the greater body of literature examining why and how certain species tolerate habitat perturbations and anthropogenically-induced alterations. The mechanics of how primate extinctions occur in disturbed areas is still relatively unknown (Irwin 2006). Studies examining the ecology of populations in altered habitats will help fill this gap in the primate literature and begin to coalesce into well-grounded conservation management for primate species in peril.

8.2 Demography at BMSR: Predictable Proximate Events

I categorized predictable proximate events as variables that affect survival of individuals in the population, have been well-documented by foreign and local Malagasy researchers, and occur on a yearly basis. Presumably, the Beza Mahafaly ring-tailed lemur population would have behavioral adaptations to accommodate these challenging, but reoccurring variables.

8.2.1 Seasonality and Reproductive Patterns.

Vegetation changes dramatically throughout the year based on annual dry and wet seasons. During a non-drought non-cyclone year, most of the rainfall occurs between October and April (Sauther *et al.* 1999). Previous research has shown that the availability of fruit and young leaves is highly correlated with rainfall (Sauther 1998). Furthermore, there are peaks of vegetation productivity coinciding with both the birth season and weaning period indicating that at this site females pattern their reproductive events to take advantage of this seasonal pattern (Sauther, 1998) (Figure 8.1). Also, it has been suggested that female dominance functions as a strategy to alleviate the high reproductive costs linked to this extremely seasonal area (Sauther 1998). One hypothesis suggests that the intense seasonality of this area has imposed significant selective pressure on this species and can be seen as a predictable annual stress (Sauther et al. 1999).



[1]Availability = Frequency of phenological trees with resources available.

Figure 8.1 Seasonality of ring-tailed lemur reproduction relative to ecological factors. (after Sauther ML, 1999).

8.2.2 Food Availability

Intimately linked to seasonality is the availability of resources for the Beza Mahafaly population of lemurs. In non-drought years, predictable blooming, ripening, and flushes of new fruits, leaves, and flowers occur throughout the year (Sauther et al. 1999, Sauther 1998, Whitelaw, unpublished data). Ring-tailed lemurs move from one available resource to another as it ripens and becomes available. Moreover, they will alter their ranging patterns drastically, and risk potentially violent intergroup encounters, to exploit the current food of choice (Sauther et al. 1999, Whitelaw unpublished data). Alteration to this food supply due to drought has been documented as severely affecting the population. A two-year drought in 1991-1992 at Beza Mahafaly had an observable effect on phenology, dramatically affecting mortality patterns, with infant mortality increasing from the non-drought year rate of 50% to about 80% (Gould et al. 1999).

8.3 Demography at BMSR: Unpredictable Proximate Events

Like predictable proximate events, I categorized unpredictable proximate events as variables that affect the survival of individuals in the population, but are not well documented by foreign or local researchers. Moreover, they do not occur on a yearly basis. Presumably, the Beza-Mahafaly ring-tailed lemur population would be unfamiliar with these events and would not have behavioral adaptations, or historical knowledge, to successfully accommodate these challenging and rare variables.

8.3.1 Cyclone and Failure of Key Resources

Cyclones are not unusual during the wet season in Madagascar. Their timing, however, can have drastic effects on the phenology of the Beza Mahafaly area. During the wet season of 2004-2005, a particularly strong cyclone struck the Beza Mahafaly Reserve during the flowering of the Tamarind trees (*Tamarindus indica* or kily). Not only was there major flooding of the Reserve, the kily flowers were also destroyed (Jacky Youssouf, unpublished data). Previous research has shown that this tree provides an important fallback resource for the lemurs (Sauther and Cuozzo, 2009). Indeed, *L. catta* consume all phenological phases (young leaves, flowers, unripe and ripe fruits). When this study began in August of 2005 (formal data collection began in October), there were no kily resources available during the peak of the dry season. Notably, this is also the end of the gestation period for females. The lemurs relied on other resources during this period, until the kily trees started producing new leaves at the beginning of the wet season. As the survival rate after a drought has indicated, females are closely tied to the variations of the environment (Sauther 1998). The birth rate following the kily failure may be further indication of this tie. Compared to earlier data, the birth rate (defined as proportion of

adult females giving birth) for 2006, following the kily failure during gestation, is much lower; 64% versus the average of 84.3% (Figure 8.2) (Gould et al. 2003).

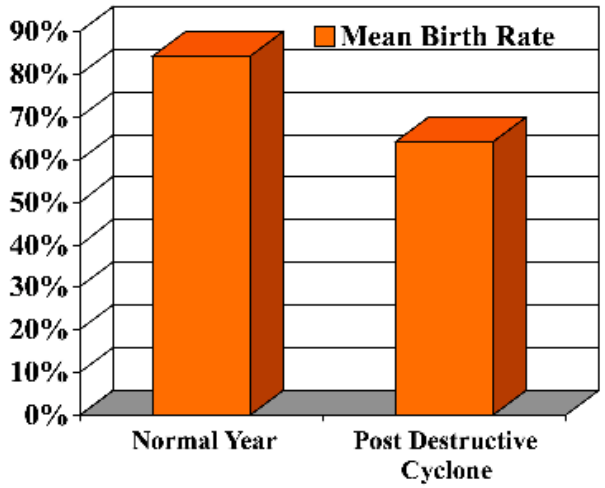


Figure 8.2 Mean birth rate in normal year versus post destructive cyclone year.

8.3.2 River crossing and flooding

The eastern border of the Reserve falls on the banks of the seasonally dry Sakamena River. During the wet season, the river periodically fills and drains depending on the rainfall in the area. Typically, it does flood and remains flowing for several weeks, if not months, at a time. During the study year, several lemur groups regularly crossed the river to access resources on the other side. The other side of the river has been severely deforested and the landscape is now covered with agricultural plots with very few arboreal refuges (Figure 8.3). Despite this deforestation, there are several patches of resources that ripen earlier than on the Reserve side (Whitelaw, unpublished data) – these are the lemurs' focus during their cross-river journeys. These resources include mangos, *Azima tetracantha*, and *Tamarindus indica.* During the river crossings, lemurs typically gallop across, engage in frenzied feeding bouts of the fruits in season

and then gallop back to the safety of the canopy. While they are across the river, they are exposed both horizontally and vertically to predators. Groups commonly encounter each other as they usually aim for the same resource, with violent intergroup encounters ensuing. During these encounters, groups frequently become separated and individuals also become isolated for portions of the day. Sometimes these isolations result in individuals missing their group's return across the river back to their home range. During one early flooding of the river, four groups became caught on the deforested side of the river since the river unexpectedly flooded during their feeding bout. It took four days for the river to retreat enough for the groups to return. During this time, I tracked the groups (Black, Green, and Light Blue) and found them huddled in shrubs up to three kilometers from their typical home range. In one dramatic isolation event, one group (not a focal group of this dissertation) became isolated for about 5 weeks in the deforested side of the river, and lost two infants and two adults during that period.

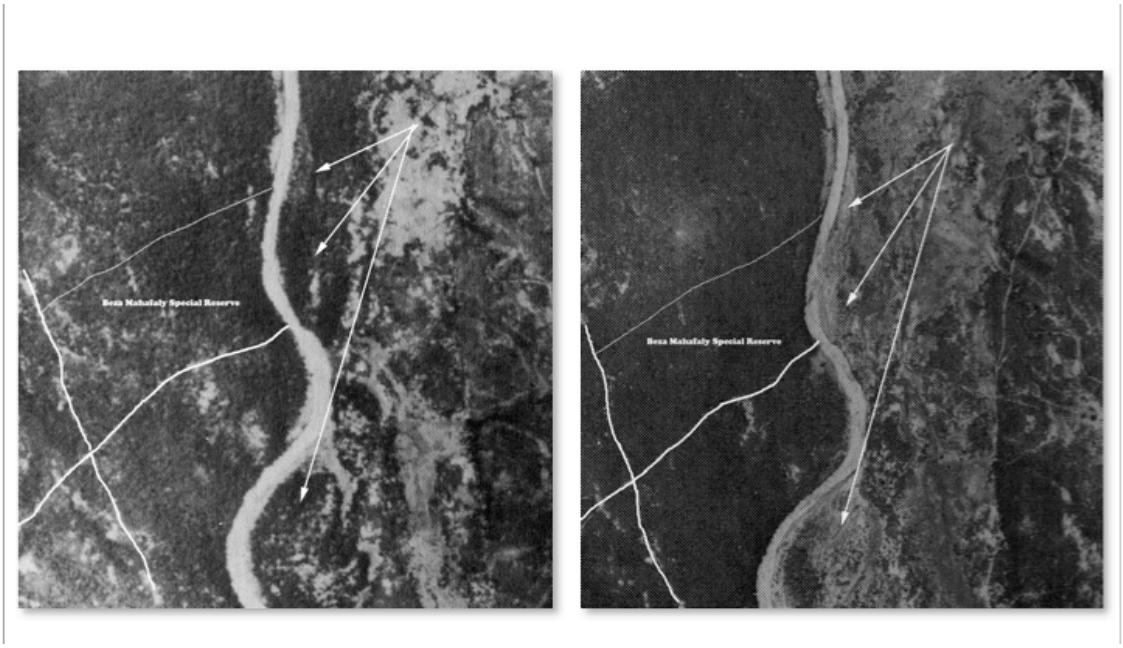


Figure 8.3 Habitat fragmentation at Beza Mahafaly over time.

8.3.3 Dogs and wild cats

Feral cats and dogs pose a deadly threat for the lemurs of Beza Mahafaly (Figure 8.4). In what seems to be an increasing problem (Sauther, pers. comm.), these animals periodically chase and frequently cause severe injury to lemurs. Researchers at Beza have confirmed two ring-tailed lemur deaths by dogs and two ring-tailed lemur deaths by a feral cat (Millette, O'Mara and Sauther unpublished data). In addition, groups are regularly chased or stalked by feral cats and dogs. For example, I observed 12 occurrences of dog packs chasing lemur groups and three cases of wild cats stalking groups during the study period (the cats are more stealthy and this may have affected observations). Moreover, these numbers are probably low since I was with each group approximately four times each month. Alarm calls and dog barks were also heard in the distance and not included in these tallies. The lemurs reacted to these predators differently. Both are greeted with alarm calls, however, when dogs were chasing the lemurs, lemurs retreated to the top of the canopy and ran quickly as far as they could – frequently losing the observer.

When the lemurs spotted a feral cat, they usually retreated to the canopy and then were quiet for hours with minimal movement. Obviously these introduced terrestrial predators are deadly to this population and not a challenge that can either be predicted or behaviorally mitigated in certain situations.

Figure 8.4 Examples of introduced lemur predators. Left: domestic dog; top right: domestic dog at night inside Parcel 1; bottom right – feral cat inside Parcel 1.

8.3.4 Habitat Differences

We have documented significant habitat differences between the protected, relatively undisturbed forest inside the Reserve, and the anthropogenically altered habitats outside of the fenced Reserve (Whitelaw and Sauther 2002, Whitelaw et al. 2005, this dissertation). These differences are obvious to the observer and include a more open understory (due to grazing and tree felling), fewer resources, and less continuous arboreal pathways (Figure 8.5). During the 9-month study period from September to June, the infant mortality rate was higher for infants primarily living in habitats outside of the Reserve (Table 8.1). There was no seasonal pattern to

these deaths. Conversely, groups consistently utilizing the protected Reserve have a higher infant survival rate (Figure 8.6). Groups outside the Reserve have more encounters with introduced terrestrial predators (Figure 8.7). Perhaps as a consequence of these encounters, of the 20 injuries observed over the study period, 75% occurred in groups outside the Reserve during the dry season (Figure 8.8). These injuries ranged from a broken tail to open wounds causing severe limping in several individuals. Life in these altered landscapes appears to be more challenging as the lemurs negotiate these variable habitats on a daily basis, yet these lemurs need to adapt actively to their unpredictable challenges.

Table 8.1 Infant survival in collared groups inside and outside Beza Mahafaly Reserve.

Groups Inside the Reserve	**Infants Born**	**Number of Infants Surviving**	**Groups Outside the Reserve**	**Infants Born**	**Number of Infants Surviving**
Green	2	1	Black	2	1
Teal	2	0	Light Blue	2	0
Blue	5	3	Yellow	3	0
Pink	4	3	Orange	5	3
Lavender	1	1	Red	3	0

Figure 8.5 Disturbed habitats around BMSR. Photos courtesy of James Millette.

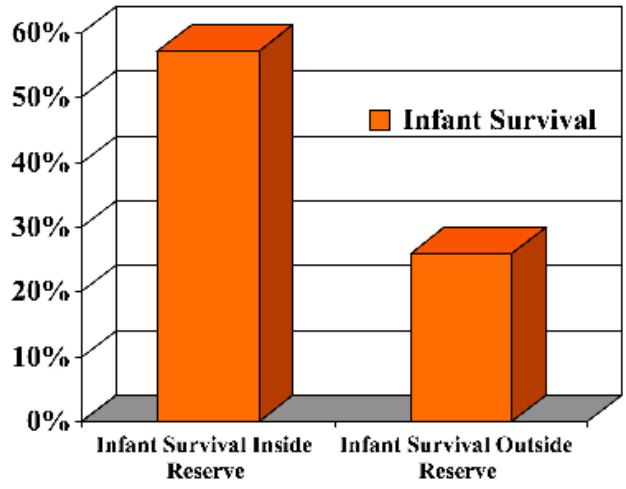


Figure 8.6 Infant survival inside and outside the Reserve.

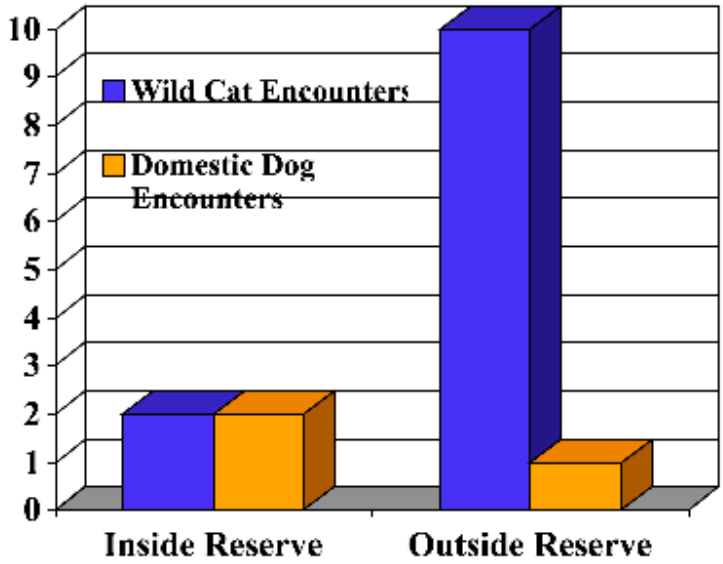


Figure 8.7 Introduced encounters with lemurs: inside versus outside the Reserve.

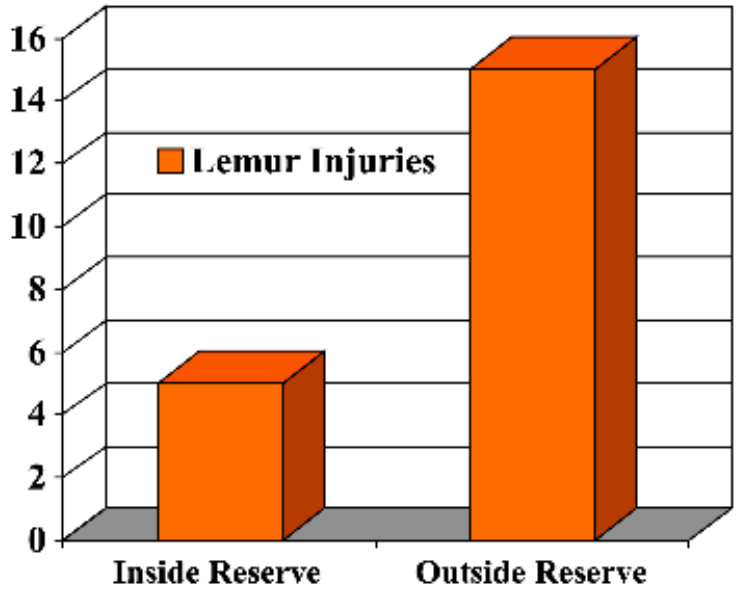


Figure 8.8 Total number of lemur injuries inside versus outside the Reserve.

8.3.5 Infant Survival Strategies

Over the study period, two interesting situations emerged in two groups being studied. First, the infant of a young and inexperienced, low ranking mother (Female 167) in Green Group, was carried by an adult female (Femaly 235) who had no infant 12 times during focal follows. The infant constantly vocalized to its mother while with the other female, but the mother failed to respond. The surrogate mother carried the infant as the group traveled and during feeding bouts. After being rejected by its mother to be carried, the infant would seek out its surrogate mother (Female 235) for traveling. On three observed occasions, a dominant female (Female 9) with an infant of her own, nursed the neglected infant of the young female. Despite this infant's survival strategies, it died after approximately seven weeks.

In the second situation, a high-ranking female (Female 110) allo-nursed the infant of a closely allied female (Female 116, Black Group) five times in Black Group. The two females were sisters. This female had recently lost her infant. The result was an accelerated growth pattern such that when the infant was 10 months old it had linear measurements similar to, and was as heavy as, a lemur nearly two years old (Sauther, unpublished data). These infant strategies of seeking out alternate mothers for nourishment and safety obviously had different results. Both examples, however, speak to adaptive behavior of infants in the uncertain and challenging journey to adulthood.

8.4 Discussion

While long-term studies are essential for understanding the demography of long-lived species, they are often only a snapshot of the true events and dynamics shaping these results. Observations of unpredictable events driving the trends seen year to year are thus important. As

highlighted here, disturbing and deadly introduced predator attacks may be an increasing factor in lemur mortality as lemurs are pushed into closer contact with humans. River crossings to highly disturbed habitat for ripe fruit can isolate groups for months if the river floods and stochastic storms can destroy the keystone resource for a population and possibly lower birth rates as a result. Altered habitats with unpredictable challenges require daily adjustments to habitat differences. Creative infant survival practices that defy usual mother-infant roles may also be an essential proximate mechanism to survive unpredictable events; this topic warrants further research and discussion. Yearly census information is clearly essential for developing a life history inventory and tracking population trends, but the unpredictable proximate variables affecting survival may be the key to truly understanding both the flexibility of primate behavior and mitigating introduced environmental pressures such as predators or habitat alterations.

In this study, documented habitat and resource abundance differences between protected and more disturbed areas have been connected to smaller home ranges, longer day ranging, more travel on the ground, and more time spent in open canopy habitats. Clearly, anthropogenic habitat alterations, coupled with stochastic changes from tropical storms, has changed the landscape both in and around BMSR and contributed to survival challenges for *L. catta* in the area. These incremental anthropogenic changes and sudden catastrophic changes create the dynamic landscape that has shaped this, and other, species. The examples described above illustrate how *L. catta* behaves, survives, and sometimes dies in the face of multiple ecological conditions. As anthropogenic changes cause more severe damage in this area, catastrophic cyclones and droughts could render this population more vulnerable since they may not have larger forest tracts to retreat to.

Finally, as anthropogenic disturbance continues to impact and shape primate behavior and ecology, primatologists are obligated to develop conservation management plans for their study populations. This discussion would become more interesting and productive by adding similar events from other taxa and geographic populations. Furthermore, collaboration among researchers will produce creative solutions to similar conservation issues.

CHAPTER 9

SYNTHESIS OF RESULTS AND IMPLICATIONS FOR PRIMATE CONSERVATION IN ANTHROPOGENICALLY DISTURBED LANDSCAPES

9.1 Summary of Results

Forest structure measurements and phenological monitoring throughout the study period at BMSR, presented in Chapter 3, indicate that anthropogenic habitat alterations have affected forest composition, stucture, and phenology at BMSR. Non-Reserve habitats tend to have little to no understory, shorter trees, but similar crown diameters and phenology scores. Edge effects such as increased food resource density and/or quality in moderately disturbed areas may be elevating resource availability in trees located near the edge zones. This summarizes the major effects in habitat composition, quality, and productivity that are apparent in the anthropogenically disturbed areas surrounding the protected area of BMSR. Furthermore, this information provides the background necessary to understand the consequences these results pose for feeding, ranging, activity patterns, social behavior, and demography that were addressed in previous chapters.

In Chapter 4, I described the effects of anthropogenically disturbed habitats on the feeding ecology of *Lemur catta*. As expected based on the habitat composition and productivity differences examined in Chapter 2, groups in Reserve and Non-Reserve habitats have divergent diets. Overall, groups tend to consume similar amounts of fruits, leaves, flowers, etc. These similarities disappear, however, when dietary diversity is examined. Groups inside the Reserve tended to rely on fewer species for the majority of their diet. Non-Reserve Groups tended to distribute their consumption across more species, consuming smaller quantities from each species. It is possible that these are more species of lower quality foods. This appears to signify

that in more marginal habitats, *L. catta* must diversify its diet and exploit foods that might not be preferred. *L. catta* inside the Reserve appears to exploit resources that are available year round in a more consistent pattern. Non-Reserve Groups, perhaps because of a less predictable, consistent supply, tend to vary their species consumption more readily. Kily was an important staple in each groups' diet. These results indicate whereas habitats that contain dense, gallery forests contain a wealth of herbs and vines, habitats in drier areas also have a variety of resources that are readily exploited by this species.

As expected, these changes in food resource distribution have affected ranging patterns, as examined in Chapter 5. Non-Reserve Groups have smaller home ranges but larger daily path lengths, relative to groups inside the Reserve. Non-Reserve Groups also tend to spend more time on the ground, despite the lack of terrestrial food resources, such as terrestrial herbs and more time in habitats with open canopies, more time traveling in open habitats, and in habitats with higher levels of disturbance (domestic animals, humans, agriculture, selective logging). Non-Reserve Groups also traveled terrestrially more than Reserve Groups. These results indicate that anthropogenic disturbance directly affects home range size, ranging, and travel patterns in *L. catta*.

In Chapter 6, I investigated the effects of habitat alterations and diet on activity patterns in each study group. Non-Reserve Groups tended to spend more time feeding and traveling and less time resting and engaging in social behavior than Reserve Groups. Notably, Non-Reserve Groups spent more time traveling at a run than did Reserve Groups.

The effects on social behavior were examined in Chapter 7. Groups outside of the protected Reserve displayed reduced group cohesion based on intragroup spacing relative to Reserve Groups, and evidence suggests this is related to dietary differences and their focus on a

higher diversity of species in their diet that are distributed less abundantly than species focused on by Reserve Groups. Non-Reserve Groups groom less, have higher rates of aggression and scentmarking, but exhibit few differences from Reserve Groups in both group structure or dominance relationships. These differences are likely a result of decreased group cohesion. The lack of social cohesion may be due to the amount of time that Non-Reserve Groups spent acquiring resources.

Chapter 8 presented results concerning patterns of mortality, injury, birth rates and survival among the study groups during the study period. Non-Reserve Groups suffered more injuries, more deaths, higher infant mortality, and more predator encounters. Moreover, this chapter discussed the predictable (seasonality) and unpredictable (destructive cyclones) that this population encountered and highlights the fact that all ecological data collected during this study year must be examined under the lens of the recent cyclone. This population does not seem to be in immediate extinction and resource stress does not appear to directly reduce survival in unprotected habitats, but resource stress may act in concert with other pressures to cause reduced viability of Non-Reserve Groups in the long-term.

Several of the results of this study do not fit neatly into predications based on some of the available theoretical perspectives. For instance, phenological surveys indicated that resource abundance was not significantly affected by disturbance outside the Reserve. These results suggest that anthropogenically altered habitats may not represent a drastically reduced quality of habitat. Furthermore, all groups except Teal were attracted to, and traveled great distances across the river, to feed in deforested habitats with heavy human traffic at similar frequencies. Perhaps habitat quality varies with habitat disturbance in a more random, rather than linear, manner (e.g. Ganzhorn 1995, Irwin 2006). That is, medium-level habitat disturbance (such as

disturbed areas with some areas of continuous traditional habitat) is often adequate, if not superior, habitat relative to either extremely degraded (e.g., drastically reduced fragments, denuded landscapes) or undisturbed areas. During this study period, altered habitats supported higher population density (for individuals, not groups), and lemurs were able to compensate for any problematic variables with alterations in behavior such as increasing feeding and ranging.

These results have several possible interpretations. First, anthropogenic habitat disturbance appears to cause an increase in density of available resources, but a possible decrease in average resource quality. This is supported by the increased population density relative to home range size of individuals outside the Reserve (therefore there are more animals using a smaller area to find food), their reliance on a more diverse diet, and biological indicators documented in other studies that are indicative of lower nutritional status such as smaller skin folds and exacerbated tooth wear and tooth loss (Cuozzo and Sauther 2004, 2006, Miller et al. 2007, Sauther et al. 2006). In this interpretation, populations are able to persist at a higher density, but still experience resource stress and they compensate for it by traveling more to access more diverse resources throughout their smaller home ranges. On the other hand, Non-Reserve habitats may harbor higher diversity, lower density, and overall lower quality resources. Therefore, groups inside the Reserve have larger home ranges because they can access higher quality resources dispersed throughout their range and they do so with a lower daily path length, more resting, and with less traveling. In contrast, Non-Reserve Groups cannot focus on preferred foods such as terrestrial herbs and leafy vines, and are forced to rely on resources that are distributed widely throughout their ranges.

In terms of the effects of these differences for these particular lemur groups and the Beza-Mahafaly ring-tailed lemur population, I believe the future of this population lies in the variables

that support population density. Groups in protected habitats that are not exposed on a daily basis to the perturbations of anthropognenic change may defend larger home ranges, and may have done so historically, to grant them access to a wider range of preferred resources (herbs, vines, fruits). This supplies them with more resources, more time to rest as their travel patterns are dictated by which resource is abundant at the time, and more time to reinforce social cohesion. In essence, they use an effort-minimizing strategy (Irwin 2006). In contrast, groups in more altered habitats are forced to renegotiate range boundaries as their habitat changes frequently in response to logging, new agricultural fields, exposure to predators, humans, and development. Their strategy is to utilize and access resources in all areas of their habitat to maximize their energy intake. These interpretations require further research, especially into the details of resource distribution and quality in each habitat to understand how these variables support the different population densities in the ring-tailed lemurs of BMSR and how it might support them in the future.

Finally, each of the results discussed here must be examined in light of the devastating cyclone Ernest, in January of 2005. As mentioned in Chapter Two, other research has shown that stochastic events such as cyclones can dramatically change feeding ecology, ranging and mortality patterns. These alterations may be both immediate and long-term. Immediate effects include extensive defoliation, tree felling, and landslides (Bellingham 2008, Catterall et al. 2008, Dittus 1985 a,b, Ratsimbazafy 2006). Longer-term effects include invasion of exotic species, alterations to phenological cycles, and force resident species to shift their diets to new species which causes ripple effects on forest ecology (Dittus 1985a,b; Ganzhorn 1995b, Ratsimbazafy 2006). At BMSR, each *L. catta* group still relied heavily on *Tamarindus indica*, however the other differences in feeding strategy may be linked to, or exacerbated by, ecological changes

resulting from Cyclone Ernest. Again, long-term monitoring will prove enlightening to more fully understand the effects of stochastic events at BMSR. Importantly, current census reports of the greater BMSR ring-tailed lemur population have shown that Light Blue Group no longer exists and the 2 females of Black Group are no longer there. In fact, several uncollared females are in Black Group, presumably emigrating from uncollared groups to the south. Clearly the ecological circumstances documented in this dissertation was the beginning of downward turns for these 2 groups.

9.2 Conservation Recommendations for *Lemur catta*

This study has quantitatively illustrated how ring-tailed lemurs can survive in anthropogenically altered landscapes, at least in the short term. In the short term, these groups make extensive behavioral and ecological changes to compensate for alterations in their habitats. During this study, injury and infant mortality rates in groups outside the Reserve illustrate that these compromises will negatively affect their long-term viability. These pressures bode poorly for these groups and their survival. Rather than suffering from outright resource scarcity, ring-tailed lemurs in the BMSR region appear to face threats that will operate in the long-term: demographic constraints, increased predation, nutritional stress from potential energy imbalance.

During the study period, ring-tailed lemurs were consistently attracted to, and sought resources in, forest edge habitats. This suggests that this species can successfully coexist in a landscape with humans. In fact, anthropogenically altered habitats might actually help these populations thrive. This is in stark contrast to some lemur species that are intolerant to even slight disturbance (White et al. 1995). I have made the assertion that this species can coexist, but this is only with the requirement that disturbance levels are controlled so that food resources are not altered beyond adequate levels. Ring-tailed lemurs in the small protected areas may have the

optimum habitat scenario due to their access to edge habitats, disturbed areas, and dense undisturbed gallery forests, especially in light of the local Mahafaly taboo against harming lemurs. In fact, the habitat just south of the Reserve where Black Group resides is an excellent example of habitat that borders highly disturbed areas (one area being the research camp and the other being agricultural fields bordering the river). Several of the earlier chapters (especially Chapter 4 on feeding ecology, highlighted how resources in Black Group's range are in some cases more similar to those inside the Reserve than to those in Light Blue Group's habitat farther away from the Reserve. If local officials were inclined to expand Parcel 1, **t**his habitat could be pReserved as a natural extension of the Reserve to support a successful breeding population that borders the Reserve**,** supporting successful male migration, keeping a larger buffer zone so that domestic and feral predators stay even further from the Reserve, and the BMSR lemur population can utilize this relatively abundant, unprotected area. I propose primary conservation management goals that will maintain the BMSR ring-tailed lemur population: 1.) preserve the large forest area protected in Parcel One and its buffer area to the north and south, particularly the areas of gallery forest; 2.) inhibit further anthropogenic disturbance from encroaching on the BMSR population, especially potential predation from domestic dogs and feral cats, and: 3.) monitor regional connectivity and disperal pathways of males along the gallery forest corridor of the Sakamena and Ehazoara watershed.

In the broader picture, it is important to recognize the other primate species in the BMSR landscape. *Propithecus verreauxi*, Verreaux's Sifaka, is at an increased disadvantage in terms of locomotor capacity to cross more disturbed habitats, even though they are perhaps less dependent on limiting resources such as fruit. This species is absent from several forest fragments utilized by ring-tailed lemurs across the river. Therefore, conservation management including both

linking gallery forest and paying close attention to connectivity of canopy and arboreal resources will not only benefit ring-tailed lemurs, but also the sifaka. These sympatric species are excellent habitat indicators in terms of folivorous/frugivorous dietary differences and leaper/quadrupedal locomotor patterns. Protecting habitat appropriate for ring-tailed lemurs will serve as a proxy for many species, including the folivorous sifaka and the fossa, *Cryptoprocta ferox*, which had traditionally been a top predator of the region but is now rarely seen.

9.3 Suggestions for Primate Conservation

Most primate species are confronted with anthropogenically altered habitats somewhere in their range, however, little is known how these alterations affect population level changes and local extinctions. Particularly problematic is the lack of specific knowledge regarding how habitat alterations affect primate behavior and ecology. We know where primates currently live, and where they used to live. The path to local extinctions remains unclear in many cases where hunting or devastating habitat changes are not the prime suspect. These holes in our research knowledge leave conservation planners ill equipped to manage populations effectively and prevent impending extinctions.

More studies should be undertaken to investigate the effects of altered forests on primate feeding ecology, ranging, activity patterns, and social behavior. Detailed understanding of behavioral profiles in relatively intact forests leaves the primatologist inadequately prepared to make decisions about a species' survival prospects. Currently, our literature base is growing and revealing great variation in how altered habitats are affecting different species in various sites. More comprehensive comparative studies investigating primates in both intact and altered forests, with emphasis on seasonality, will make it possible to begin to see patterns in resource distribution and their effects on primate behavior and the process of extinction. These studies are

at the core of anthropology: adaptation, behavior, ecology, and extinction. A holistic approach to understanding the nuances of each phase will illuminate not only a theoretical understanding, but allow informed decisions by conservation planners for our non-human primate relations.

Contributions of this dissertation to the major themes discussed in the first chapter are discussed here:

How do Primates Utilize Anthropogenically Fragmented Landscapes? - Unfortunately, there is little comprehensive research about primate movements and dispersal in anthropogenically altered landscapes. The matrix – the habitat between established home ranges and, in altered landscapes, the most degraded and unrecognizable habitat – can be a mosaic of uninhabitable space and patchy arboreal habitat. Clearly, it is imperative to understand how primates utilize this space and their ranging patterns within it, if at all. The results presented here indicate that ring-tailed lemurs utilize the matrix, albeit at a run. They cross these matrices to access highly sought after resources. Behaviors, such as vigilance and running, indicate that it is not without a cost that these individuals access these resources. Dispersal appears to be possible in the anthropogenically altered habitats south of the protected area. While the appearance of a few uncollared individuals supports this, it is also apparent that intergroup transfers are far more dynamic and common in areas where groups are more densely populated, e.g., inside the Reserve. Emigrations of three males from Teal and the fission of Green Group along with the emigration of two males illustrates that intergroup activity is far more active when groups are within relatively undisturbed areas. Because metatpopulation theories assume patch residence for individuals, with only some dispersal between matrix habitats, this approach may be appropriate for modeling this population. Models must be approached with caution due to the number of assumptions that must be made, however, the riverine corridor, with fragments and

continuous forest might be an appropriate landscape model for the metapopulation approach. To adequately apply this theory, the scope of research must expand beyond Parcel 1 and surrounding habitats to fragments across the river and into the Ehazoara watershed. The gallery forest corridor is likely to be the prime dispersal corridor for the greater Beza Mahafaly ring-tailed lemur population.

Processes of extinction in small populations – Extinction is fairly easy to document after the fact, but the more difficult data are the processes leading up to the disappearance of a species. Researchers have very few data concerning the timeline of events and behavioral ecology leading up to extinction events (Caughley 1994, Lande 1998, Pimm et al. 1988). Study groups in this dissertation suggested that ring-tailed lemurs outside the Reserve suffer from higher injury and predation rates, higher infant mortality, and lower birth rates. These data, in concert with higher rates of feeding and traveling, may indicate an ecologically stressed population. Are these the processes of local extinction in a small population? Comprehensive monitoring over time will determine if these variables, rather than outright starvation, are indicators of population failure in this population.

Assimilation of BMSR (habitat) and Larger Landscape Models – As more data are collected, integration of habitat based data (i.e., the effects of habitat disturbance) and landscape-oriented (i.e. metapopulation focused) models will be essential to understanding the dynamics of anthropogenically altered landscapes on populations (Armstrong 2005, Franken and Hik 2004, Larsen et al. 2004, Lawes et al. 2000). The advancement of these two fields, and conservation as a whole – habitat based research and landscape ecology – depends upon the integration of these fields. Data presented here indicate that habitat-based research and integration of a larger, landscape based approach will impact the conservation of species and that habitat- and

landscape-based perspectives impact the BMSR ring-tailed lemur population. Fundamentally, anthropogenic habitat change has altered habitat structure, resource base and home range for ring-tailed lemurs in and around BMSR. These perturbations have reverburations for the population as a whole in terms of spatial ecology, their resource base, and the challenges for dispersing individuals. To project this population's future, it will be imperative to consider both the habitat-based data, and the landscape information; they are inseparable and interconnected. It seems only logical that both specific habitat data and landscape-level ecology data are necessary to predict adequately the future dispersal and population trajectory predictions.

Implications of Behavior and Local Extinctions – Behavioral ecology as a field currently lacks comprehensive studies examining how social behaviors change in anthropogenically altered habitats and how they interplay with population processes leading to local extinctions (Anthony and Blumstein 2000). This dissertation research unveiled several effects of anthropogenically altered habitats on social behavior of ring-tailed lemurs. For example, Non-Reserve Groups were found to scentmark more, engage in more aggressive behaviors, and groom less. It remains unclear, however, how these hallmark behaviors may impact population viability in the long-term. The most important change that was recorded during the study period was the lack of group cohesion. Individuals in Non-Reserve Groups were far more likely to be farther apart during the active period. Other research has shown that Groups that exhibit reduced cohesion are more susceptible to predation incidents during the day (Hamilton 1971, Isbell 1994, Irwin 2006). Constraints on group cohesion and conspecific attraction can be indicators of habitat quality (Reed and Dobson 1993). Continuing the long-term monitoring of the BMSR population, including behavioral studies, will provide significant insight regarding the interplay of social behaviors and small populations processes leading to local extinction.

How do we judge population's 'success'? – There are several ways to examine populations in anthropogenically altered habitats and derive conclusions regarding their viability. These include population density (increased population density suggest habitat and population viability) presence of infants and juveniles, individual body weights that are equivalent to those in protected areas, ration of females to males, and so forth. Johns and Skorupa (1987) analyzed 21 primate species to construct an index representing a rapid assessment of susceptibility to disturbance. In essence, the index measured the ratio of abundance in disturbed areas to abundance in undisturbed areas. There were other variables involved as well, such as diet (the index increased with increasing frugivory, and this was mitigated by body size as well: larger bodied species are more vulnerable to disturbance). Their results may not be as widely applicable as they were presented to be. Ring-tailed lemurs in the BMSR region would score highly on Johns and Skorupa's survival index because population density relative to home range size is higher in altered habitats than in protected areas. Data presented in this dissertation, however, may negate this as behavioral data revealed ecological compromises that might threaten the viability of groups living in unprotected areas. Furthermore, these behavioral data, coupled with increased incidents of predator encounters and sustained injuries, lower birth rates and infant survival, and very few number of females in Non-Reserve groups are significant variables that may lead to local extinctions in anthropogenically altered landscapes despite these groups' higher population densities. Thus, conservation officials must be wary of attributing higher population density to population success and viability; there may be less obvious factors at play that may significantly affect population viability. Moreover, while individual groups may have higher population density, group density overall may be reduced therefore limiting dispersal potential from neighboring populations due to inhospitable matrix habitat. Long-term,

comprehensive population monitoring will be crucial for determining the underlying factors contributing to population viability or demise.

While attempts have been made to establish indices and frameworks to assess primate species' viability in disturbed habitats, primatologists have a daunting amount of detailed research ahead before we can achieve an adequate understanding of the processes leading to extinction. This dissertation presents results that contribute to the understanding of underlying processes of one primate species' adaptation to anthropogenic habitat alteration. Researchers have a long way to go to understand the intricacies of variation in how animals survive in disturbed landscapes. Results presented here shed some light on the issues that need to be examined. Future research should focus on investigating more species' reactions to marginal and altered landscapes to assess the range of variables that these ecological factors can affect and integrating theoretical frameworks to find a format that fits the current needs of primate behavioral ecology in a world with increasingly altered habitats.

This is only the beginning, however, and further research is necessary to fully understand this complex part of the evolutionary trajectory. Future research is essential to help prevent the catastrophic loss of primate populations in preventable situations and should focus on: 1.) examining more species in diverse habitats to evaluate the scope of primates' responses to habitat degradation, and; 2.) establishing and applying valid theoretical perspectives that will allow researchers to work under the same set of assumptions and understanding and advance the science of conservation.

9.4 Directions for Future Research

This study is one of the first to investigate the pressures of anthropogenic habitat disturbance and their effects on the behavioral ecology of a primate species in the wild. Moreover, this dissertation documents the feeding and ranging ecology of a primate after a destructive cyclone altered the natural phenological cycles of plants in the region. This combination of anthropongenic and stochastic disturbance is unique. While this project attempts to answer significant questions regarding the adaptive capacity of ring-tailed lemurs, because of the slow life history of primates, the infinite number of habitat variables that can be measured, and the slow rate of change in ecosystems in response to perturbations (both natural and anthropogenic), researchers must continue to monitor these groups and the population as a whole to more comprehensively address the questions of adaptability and viability. Specifically, additional long-term research will develop a more complete picture of how ring-tailed lemurs will fare in altered landscapes and in understanding the most valuable way to manage the current protected areas. In 2009, under a national movement to expand protected areas, BMSR has been expanded from approximately 600 to almost 8,000 hectares. Within the expansion of the Reserve, there are different categories of land use ranging from limited grazing to highly controlled use areas (Figure 9.1) (Youssouf 2009).

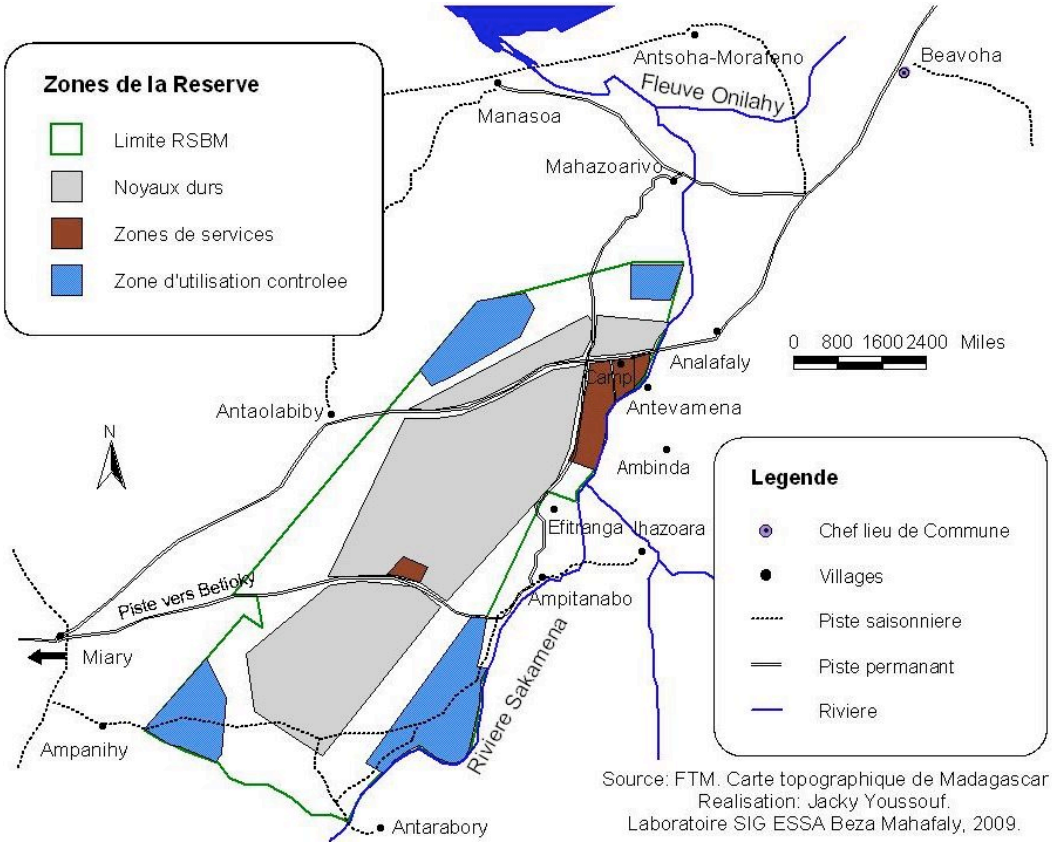


Figure 9.1 Recent expansion of BMSR (Youssouf, 2009). Map used with permission of the author.

It is my recommendation that the following avenues of research be examined:

1.) Continued Population Monitoring of Ring-tailed Lemurs in and around BMSR – It will be valuable to maintain the current research program at BMSR and continue to integrate more comprehensive behavioral data collection to monitor the short-term behavioral shifts documented in this study. This is currently being undertaken by several graduate students and the Ring-tailed Lemur Biology Project led by Drs. Sauther and Cuozzo.

2.) *Investigating the effects of anthropogenic habitat change on food chemistry and quality* – This study documented the dietary shift of Non-Reserve Groups focusing on a more diverse array of food species than Reserve Groups. To fully understand how this different

strategy affects energy intake and supports their other behavioral shifts, it will be enlightening to examine the chemical properties of these food items.

3.) *Continued monitoring of health and disease patterns in the BMSR population* – Recent studies have emphasized the importance of biological assessments of populations and the wealth of data that can be acquired and correlated to behavioral ecological data (Chapman et al. 2005, Junge and Sauther 2006, Loudon 2009). Continuing and expanding the collection of biological data will be insightful in its quantitative contribution to the assessment of behavior, feeding, ranging, and demographic patterns in the BMSR ring-tailed lemur population.

4.) *Integrating BMSR Ring-tailed Lemur Population Patterns into Models* - Expanding the current knowledge of ring-tailed lemur population and including groups along the gallery forest corridor of the Sakemena, Ehazoara, and Onilahy watersheds will provide valuable insight into the population dynamics of the larger ring-tailed lemur population in southwestern Madagascar. Censusing these riverine networks in the larger landscape, including patch characteristics such as species richness and composition, and examining colonization rates will allow the first metapopulation analysis of primates in Madagascar. Utilizing well established theoretical frameworks, such as metapopulation dynamics, will be invaluable in determining long-range viability of landscape level populations. Combining the detailed knowledge of the BMSR population with larger landscape level studies is a potent combination that will advance conservation science for primatology.

5.) *Continuing Comparative Behavioral Ecological Studies of other Species* – This dissertation has only augmented our awareness of the behavioral ecological processes affecting the population dynamics for one species in the anthropogenically altered habitats of the BMSR region: *Lemur catta*. These alterations do not target one species at a time, thus it is unwise to

generalize conclusions reached in this study to other primate species in the same habitat. Sweeping statements and recommendations are ill-advised. What will be far more powerful are similar comparative studies on the other primate species in the area. These studies, in turn, will lend broader knowledge of primate adaptive strategies in challenging landscapes from a variety of primate guilds with different activity patterns, locomotor adaptations, dietary strategies, and microhabitats. These studies will contribute to the great need of establishing a broad body of work examining how primates are coping, adapting, succeeding, or failing in anthropogenically altered habitats.

REFERENCES

Aberg J, Jansson G. Swenson JE, and P Angelstam. 1995. The effect of matrix on the occurrence of hazel mouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia 103: 265-269.

Altmann J, and P Muruthi. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. American Journal of Primatology 15: 213-221.

Altmann J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227-267.

Andersen M, Thornhill A, and H Koopowitz. 1997. Tropical Forest Disruption and Stochastic Biodiversity Losses. In: Tropical Rainforest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Laurance WF, Bierregaard RO, editors. University of Chicago Press, Chicago.

Anderson J, Rowcliffe JM, and G Cowlishaw. 2007. Does the matrix matter? A forest primate in a complex agricultural landscape. Biological Conservation 135: 212-222.

Anthony LL, and DT Blumstein. 2000. Integrating behavior into wildlife conservation: The multiple ways that behavior can reduce N_e. Biological Conservation 95: 303-315.

Armstong DP 2005. Integrating the metapopulation and habitat paradigms for understanding broadscale declines of species. Conservation Biology 19: 1402-1410.

Atkinson CT, Woods KL, Dusek RJ, Sileo LS, and WM Iko. 1995. Wildlife disease and conservation in Hawaii: Pathogenicity of avian malaria in experimentally infected Iiwi. In: Parasitology: Ecology of wildlife host-parasite interactions. Grenell BT, and Chappell LH, editors. Cambridge University Press pp: 59- 69.

Atmar W and BD Patterson. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologica 96: 373-382.

Augsberger CK. 1981. Reproductive synchrony of a tropical shrub: Experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62: 775-788.

Barnes RFW. 1990. Deforestation trends in tropical Africa. African Journal of Ecology 28: 161-173.

Barton RA, Byrne RW, and A Whiten. 1996. Ecology, feeding competition and social structure in baboons. Behavioral Ecology and Sociobiology 38: 321-329.

Behie AM, and MSM Pavelka. 2005. The short-term effects of a hurricane on the diet and activity of black howlers (*Alouatta pigra*) in Monkey River, Belize. Folia Primatologica 76:1-9.

Bekoff M. 1984. Social Play Behavior. Bioscience 34: 228-233.

Bellingham PJ. 2008. Cyclone effects on Australian rain forests: An overview. Austral Ecology 33: 580-584.

Bender DJ, Contreras TA, and L Fahrig. 1998. Habitat Loss and Population Decline: A Meta-Analysis of the Patch Size Effect. Ecology 79 (2): 517-533.

Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conservation Biology 12: 380-389.

Bennett EL, and Z Dahaban. 1995. Wildlife responses to disturbance in Sarawak and their implications for forest management. In: Primate RB, Lovejoy TE (eds.), Ecology, conservation, and management of southeast Asian rainforests. New Haven: Yale University Press.

Berenstain L. 1986. Responses of long-tailed macaques to drought and fire in eastern Borneo: A preliminary report. Biotropica 18:257-262.

Bicca-Marques JC. 2003. How do howlers cope with habitat fragmentation? In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 283-293.

Bierregaard Jr. RO, Gascon C, Lovejoy TE, and R Mesquita. 2001. Lessons From Amazonia: The Ecology and Conservation of a Fragmented Forest. New Haven: Yale University Press.

Bierregaard RO and TE Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazónica 19: 215- 241.

Bierregaard RO and VH Dale. 1996. Islands in an ever-changing sea: The ecological and socioeconomic dynamics of Amazonian rainforest fragments. In: J Schelhas and R Greenberg (eds.) Forest Patches in Tropical landscapes. California: Island Press. Pp. 187-204.

Binggeli P. 2003. Introduced and invasive plants. In: The Natural History of Madagascar, SM Goodman and JP Benstead, editors. University of Chicago: Chicago. Pp. 257-268.

Boinksi S. 1994. Costa Rican squirrel monkey: Waltzing towards extinction. American Journal of Primatology 33: 196-197.

Bowen-Jones E, and S Pendry. 1999. The threat to primates and other mammals from the bushmeat trade in Africa, and how this threat could be diminished. Oryx 33: 233-246.

Box H. 1991. Primate Responses to Environmental Change. Chapman and Hall, London.

Breugeman JA. 1978. The Function of adult play in free-ranging *Macaca mulatta*. New York: Academic Press.

Brockman DK, Godgrey LR, Dolar LJ, and J Ratsirarson. 2008. Evidence of Invasive *Felis Silvestris* Predation on *Propithecus verrauxi* at Beza Mahafaly Special Reserve, Madagascar. International Journal of Primatology 29: 135-152.

Brokaw N, and J Thompson. 2000. The H for DBH. Forest Ecology and Management. 129: 89–91.

Bronikowski A, and J Altmann. 1996. Foraging in a variable environmental: Weather patterns and the behavioral ecology of baboons. Behavioral Ecology and Sociobiology 39: 11-25.

Brown JH, and A Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58: 445-449.

Brugiere D, Gautier JP, Moungazi A, and A Gautier-Hion. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. International Journal of Primatology 23: 999-1024.

Bruna EM. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. Oecologia 132: 235-243.

Budnitz, N. 1976. Feeding behavior of *Lemur catta* in different habitats. Unpublished Ph.D. dissertation. Duke University.

Budnitz N, and K Dainis. 1975. *Lemur catta*: Ecology and behavior. In: Lemur Biology. Tatersall I, Sussman RW, eds. Pp 219-236. Plenum Press, New York.

Burkey TV. 2003. Edge Effects in Seed and Egg Predation at Two Neotropical Rainforest Sites. Biological Conservation 66: 139-143.

Caro T. 1998. Behavioral Ecology and Conservation Ecology. Oxford University Press, New York.

Caro T. 1999. The behaviour-conservation interface. Trends in Ecology and Evolution 14: 366-369.

Catterall CP, McKenna S, Kanowski J, and SD Piper. 2008. Do cyclones and forest fragmentation have synergistic effects? A before-after study of rainforest vegetation structure at multiple sites. Australian Ecology 33: 471-484.

Caughley G. 1994. Directions in Conservation Biology. Journal of Animal Ecology 63: 215–244.

Chapman CA and SR Balcomb. 1998. Population Characteristics of Howlers: Ecological Conditions or Group History. International Journal of Primatology 19: 385-403.

Chapman CA, and CA Peres. 2001. Primate conservation in the new millennium: The role of scientists. Evolutionary Anthropology 10: 16-23.

Chapman CA, and JE Lambert. 2000. Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. American Journal of Primatology 50: 169-185.

Chapman CA, and LJ Chapman 2000. Determinants of Group size in primates: The importance of travels costs. In: S Boinski and PA Garber (eds.); On the Move: How and Why Animals Travel in Groups. Chicago: University of Chicago Press. Pp. 24-42.

Chapman CA, and LJ Chapman. 1995. Survival without dispersers: seedling recruitment under parents. Conservation Biology 9: 675-678.

Chapman CA, Balcomb SR, Gillespie TR, Slorupa JP, and TT Struhsaker. 2000. Long- term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. Conservation Biology 14: 207-217.

Chapman CA, Chapman LJ, and KE Glander. 1989. Primate populations in northwestern Costa Rica: potential for recovery. Primate Conservation 10: 37-44.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, and LR McDowell. 2004. Predicting folivorous primate abundance: Validation of a nutritional model. American Journal of Primatology 62:55-69.

Chapman CA, Gautier-Hion A, Oates JF, and DA Onderdonk. 1999. African primate communities: determinants of structure and threats to survival. In: Fleagle JG, Janson CH, and KE Reed (eds.), Primate communities. Cambridge: Cambridge University Press.

Chapman CA, Gillespie TR, and TL Goldberg. 2005. Primates and the ecology of their infectious disease: How will anthropogenic change affect host-parasite interactions? Evolutionary Anthropology 14: 134-144.

Chapman CA, Lawes JM, Naughton-Treves L, and TR Gillespie. 2003. Primate survival in community-owned forests fragments: Are metapopulation models useful amidst intensive use? In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 63-78.

Chapman LJ, Chapman CA, and RW Wrangham. 1992. *Balanites wilsoniana*: Elephant dependent dispersal? Journal of Tropical Ecology 8: 275-283.

Cheney DL, and RM Seyfarth. 1987. The influence of interGroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21: 375-386.

Chiarello AG, and FR de Melo. 2001. Primate population densities and sizes in Atlantic forest remnants of Northern Espirito Santo, Brazil. International Journal of Primatology 22: 379 – 396.

Collinge SK. 2001. Spatial ecology and biological conservation. Biological Conservation 100: 1-2.

Connor EF, and ED McCoy. 1979. The statistics and biology of the species-area relationship. American Naturalist 113: 791-833.

Cords M, and TE Rowell. 1986. Group fission in blue monkeys of the Kakamega forest, Kenya. Folia Primatologica 46: 70-82.

Cowlishaw G, and R Dunbar. 2000. Primate conservation biology. University of Chicago Press: Chicago.

Cowlishaw G. 1999. Predicting the pattern of decline of African primate diversity: An extinction debt from historical deforestation. Conservation Biology 13: 1183-1193.

Crockett CM and JF Eisenberg. 1986. Howlers: Variations in Group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham R, and Struhsaker TT. (eds.) Primate Societies, University of Chicago Press, Chicago, pp. 54-68.

Cuarón AD. 2000. A Global Perspective on Habitat Disturbance and Tropical Rainforest Mammals. Conservation Biology 14: 1574-1579.

Cullen Jr. L, Bodmer RE, and C Valladares Pádua. 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biological Conservation 95: 49-56.

Cunningham SA. 2000. Depressed pollination in habitat fragments causes low fruit set. Proceedings, Royal Society of London, Series B 267: 1149-1152.

Cuozzo FP, and ML Sauther. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids. Journal of Human Evolution. 46: 623-631.

Cuozzo FP and ML Sauther. 2006. Severe Wear and Tooth Loss in Wild Ring-Tailed Lemurs (*Lemur catta*): A Function of Dental Structure, Feeding Ecology, and Life History. Journal of Human Evolution 51: 490-505.

Daehler C. 2003. Performance comparisons of co-occuring native and alien invasive plants: Implications for Conservation and Restoration. Annual Review of Ecology, Evolution, and Systematics 34: 183-211

Dahdouh-Guebas F, and N Koedam. 2006. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): Solutions to ambiguous field situations and description

of the PCQM protocol. Forest Ecology and Management. 228: 1–18.

Decker BS. 1994. Effects of Habitat Disturbance on the Behavioral Ecology and demographics of theTana River Red Colobus (*Colobus badius rufomitratus*). International Journal of Primatology 14: 703-737.

Deghan A. 2003. The behavior of extinction: Predicting the incidence and local extinction of lemurs in fragmented habitats of southeastern Madagascar. PhD Dissertation. University of Chicago, Chicago, Illinois.

Dewar RE, and AF Richard. 2007. Evolution in the hypervariable environment of Madagascar. PNAS 104: 13723-13727.

DeWitt TJ, A Sih, and DS Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13: 1–8.

Diamond, JM. 1975. The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves. Biological Conservation. 7: 129–46.

Didham RK, and JH Lawton. 1999. Edge sructure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31: 17-30.

Dirzo R, and A Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273-287 in PW Price, PW Lewinsohn, GW Fernandes, and WW Benson (eds.) Plant animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York.

Dittus WPJ. 1985a. The Influence of Cyclones on the dry Evergreen Forest of Sri Lanka. Bioropica 17: 1-14.

Dittus WPJ. 1985a. The cyclones on the dry evergreen forest of Sri Lanka. Biotropica 17: 1-14.

Dittus WPJ. 1985b.The influence of leaf-monkeys on their feeding trees in a cyclone-disturbed environment. Biotropica 17: 100-106.

Donlan DJ, Tershy BR, Campbell K, and F Cruz. 2003. Research for Requiems: the Need for More Collaborative Action in Eradication of Invasive Species. Conservation Biology 17: 1850-1851.

Donovan TM, Jones PW, Annand EM, and FR Thompson III. 1997. Variation in local scale edge effects: mechanisims and landscape context. Ecology 78: 2064-2075.

Dunbar RIM. 1992. Time: A hidden constrint on the behavioral ecology of baboons. Behavioral ecology and Sociobiology 31: 35-49.

Dunham AE, Erhart EM, Overdorff DJ, and PC Wright. 2008. Evaluating effects of deforestation, hunting, and El Nino events on a threatened lemur. Biological Conservation 141: 287-297.

Epple G. 1986. Communication by chemical signals. In G Mitchell and J Erwin (eds.): Comparative Primate Biology. Volume 2A: Behavior Conservation and ecology: Alan R. Liss, pp. 531-580.

Erhart EM. 2008. Rates of Agonism by Diurnal Lemuroids: Implications for Female Social Relationships. International Journal of Primatology 25: 5–17.

Estrada A, and R Coates-Estrada 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology 17: 759-783.

Estrada A, Juan-Solano S, Martinez TO, and R Coates-Estrada. 1999. Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living a forest fragment at Los Tuxtlas, Mexico. American Journal of primatology 48: 17-183.

Estrada A, Mendoza A, Castellanos L, Pacheco R, van Belle S, García Y, and D Muñoz. 2002. Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. American Journal of Primatology 58: 45-55.

Everham EM III, and NVL Brokaw. 1996. Forest damage and recovery from catastrophic wind. Botanical Review 62:113-185.

Fa JE, Juste J, Perez del Val J. and J Castroviejo. 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conservation Biology 9: 1107-1115.

Fa JE, Garcia Yuste JE, and R Castelo. 2000. Bushmeat Markets on Bioko Island as a Measure of Hunting Pressure. Conservation Biology 14: 1602-1613.

Fa JE, Peres CA, and J Meeuwig. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conservation Biology 16: 232-241.

Fimbel C. 1994. Ecological correlates of species success in modified habitats may be disturbance and site-specific: the primates of Tiwai Island. Conservation Biology 8: 106-113.

Fitzgibbon CD. 1997. Small mammals in farm woodlands: The effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology 34: 530-539.

Fleagle JG, CH Janson, and KE Reed. 1999. Spatial and temporal scales in primate community structure. In Fleagle JG, CH Janson, KE Reed (eds.), Primate Communities, Cambridge University Press, Cambridge, pp. 284-288.

Fleagle JG. 1999. Primate Evolution and Adaptation. New York: Academic Press.

Franken FJ, and DS Hik. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology 73: 889-896.

Fuentes A, Suaryana KG, Artaputra IGA, Haryaputra IDK, and ALT Rompis. 2001. The behavioral ecology and distribution of long-tailed macaques in Bali, Indonesia. American Journal of Physical Anthropology Suppl. 32: 66.

Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, and D Zinner. 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. Conservation Biology 13: 794-804.

Ganzhorn JU, Goodman SM, and A Dehgan. 2003. Effects of forest fragmentation on small mammals and lemurs. In SM Goodman and JP Benstead, eds.: The Natural History of Madagascar. Chicago: University of Chicago Press, pp. 1228-1234.

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Rakotondravony D, Rakotosamimanana B, and D Vallan. 2000a. Vertebrate species in fragmented littoral forests of Madagascar. In WR Lourence and SM Goodman, eds.: Diversite et Endemisme a Madagascar. Paris: Societe de Biogeographie, pp. 155-164.

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Rakotondravony D, and B Rakotosamimanana. 2000b. Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In G Rheinwald, ed.: Isolated Vertebrate Communities in the Tropics. Bonn: 4th International Symposium pp. 265-272.

Ganzhorn JU. 1995a. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76: 2084-2096.

Ganzhorn JU. 1995b. Cyclones over Madagascar: Fate or fortune? Ambio 24: 124-125.

Gascon C, Lovejoy TE, Bierregaard Jr. RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, and S Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91: 223-229.

Gascon C, Williamson GB, and GAB da Fonseca. 2000. Receding forest edges and vanishing Reserves. Science 288- 1356-1358.

Gehring TM, and RK Swihart. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109: 283-295.

Gigord L, Picot F, and JA Shykoff. 1999. Effects of habitat fragmentation on *Dombeya acutangula* (Sterculiaceae) a native tree on La Reunion (Indian Ocean). Biological Conservation 88: 43-51.

Gilbert KA, and EZF Setz. 2001. Primates in a fragmented landscape: Six species in central Amazonia. In RO Bierregaard jr., C Gascon, TE Lovejoy and RCG Mesquite, eds. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. New Haven: Yale University Press, pp 262-270.

Gilbert KA. 2003. Primates and fragmentation of the Amazon forest. In LK Marsh (ed.): Primates in Fragments: Ecology and Conservation. New York: Kluwer, pp. 145-157.

Gilpin ME and JM Diamond. 1980. Subdivision of nature Reserves and the management of species diversity. Mature 285: 567-568.

Godfrey LR and MT Irwin. 2007. The Evolution of Extinction Risk: Past and Present Anthropogenic Impacts on the Primate Communities of Madagascar. Folia Primatologica 78: 405-419.

Goldsmith ML, Nkurunungi, J, and CB Stanford. 1999. Gorilla behavioral ecology: Effects of altitudinal changes on highland/lowland populations. American Journal of Physical Anthropology. Suppl 28: 137.

Goodall J. 1986. Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, MA.

Goodman SM, and O Langrand. 1996. A high mountain population of the ring-tailed lemur, *Lemur catta*, on the Andringitra Massif, Madagascar. Oryx 30: 259-268.

Goodman SM. 2003. Predation on lemurs. In SM Goodman and JP Benstead (eds.): The Natural History of Madagascar. Chicago: Univeristy of Chicago Press, pp. 1221-1228.

Goosem M. 1997. Internal Fragmentation: The Effects of Roads, Highways, and Powerline Clearings on Movements and Mortality of Rainforest Vertebrates. In: Tropical Rainforest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Laurance WF, Bierregaard RO, editors. University of Chicago Press, Chicago.

Gordon DR. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. Ecological Applications 8: 975-989.

Gorman ML, and MGL Mills. 1984. Scent marking strategies in hyaenas (Mammalia). Journal of Zoology (London) 202: 535-547.

Gosling LM. 1990. Scent marking by resource holders: Alternative mechanismas for advertising the costs of competition. In: DW Macdonald, D Muller-Schwarze and SE Natynczuk (eds.): Chemical Signals in Verterbrates 5. Oxford: Oxford University Press, pp. 315-328.

Gould L. 1989. Infant social development and alloparenting in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. M.A. thesis, University of Alberta, Alberta, Canada.

Gould L. 1994. Patterns of affiliative behavior in adult male ring-tailed lemurs (*Lemur catta*) at

the Beza Mahafaly Special Reserve, Madagascar. Ph.D. dissertation, Washington Univeristy, St. Louis, MO.

Gould L. 1997. Intermale affiliative relationships in ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. Primates 38: 15-30.

Gould L. 2006. *Lemur catta* Ecology: What We Know and What We Need to Know. In: Lemurs: Ecology and Adaptation. Gould L, and ML Sauther, eds. University of Chicago Press, Chicago. Pp. 255-274.

Gould L, and DJ Overdorff. 2002. Adult male scent-marking in *Lemur catta* and *Eulemur fulvus rufus*. International Journal of Primatology 23: 575-586.

Gould L, and ML Sauther. 2007. Ani-Predator Strategies in a diurnal Prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Resere, Madagascar. In Primate Anti-Predator Strategies. Gursky SL, and Nekaris KAI (editors). Springer, New York Pp. 275-288.

Gould L, Sussman RW, and ML Sauther. 1999. Natural Disasters and Primate Populations: the Effeects of a 2-Year Drought on a Naturally Occurring Population of Ring-Tailed Lemurs (*Lemur catta*) in Southwestern Madagascar. International Journal of Primatology 20: 69-84.

Gould L, Sussman RW, and ML Sauther. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. American Journal of Physical Anthropology 120: 182-194.

Grassi C. 2002. The Behavioral Ecology of *Hapalemur griseus griseus*: The influences of microhabitat and population density on the small-bodied folivore (Madagascar). Ph.D. Dissertation, University of Texas at Austin.

Green GM, and RW Sussman. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. Science 248: 212-215.

Groombridge B. 1992. World Conservation Monitoring Centre, British Museum, and World Conservation Union. Global biodiversity status of the earth's living resources: a report. Chapman & Hall, London.

Gross DR. 1975. Protein capture and cultural development in the Amazon Basin. American Anthropologist 77: 526-549.

Hamilton WD. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 3: 295-311.

Hanski I and D Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: Metapopulation Biology: Ecology, Genetics, and Evolution. Hanski, I., Gilpin, M.E., eds. Pgs 5-26. Academic Press, San Diego, CA.

Hanski I, and ME Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society. 40: 3-16.

Hanski I, and ME Gilpin. 1996. Metapopulation biology: ecology, genetics, and evolution. Academic Press, London.

Hanski I. 1991. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution 9: 131-135.

Hanski I. 1998. Metapopulation dynamics. Nature 396: 41-49.

Harrinton JE. 1977. Discrimination between males and femailes by scent in *Lemur fulvus*. Animal Behavior. 25: 147-151.

Harris LD. 1988. Edge effects and conservation of biotic diversity. Conservation Biology 2: 330-332.

Harrison S. 1994. Metapopulations and conservation. In: PJ Edwards, RM May and NR Webb (eds.): Large-Scale Ecology and Conservation Biology. London: Blackwell Scienrific Publications. Pp: 111-128.

Heckman KL, Rasoazanabary E, Machlin E, Godfrey LR, and AD Yoder. 2006. Incongruence between genetic and morphological diversity in *Microcebus griseorufus* of Beza Mahafaly. BioMed Central; Evolutionary Biology 6: 98.

Hemingway CA, and DJ Overdorff. 1999. Sampling effects on food availability estmates: Phenological method, sample size, and species composition. Biotropica 31: 354-364.

Hobbs RJ. 1988. Disturbance regimes in remnants of natural vegetation. In: Saunders DA, Arnold GW, Burbridge AA, and AJM Hopkins (eds). Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons, Chipping Norton, Australia.

Holyoak M, Leibold MA, and RD Holt. 2005. Metacommunities: Spatial Dynamics and Ecological Communities. Chicago: University of Chicago Press.

Hooge PN and B Eichenlaub. 1997. Animal movement extension to ArcView. Ver. 2.0 Alaska Science Center – biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

Horn HS and RH MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53: 749-752.

Huss-Ashmore R. 2000. Theory in Human Biology: Evolutionary, Ecological Adaptability and Variation. In: Stinson S, Bogin B, Huss-Ashmore, O'Rourke D, editors. Human biology: An evolutionary and biocultural perspective. 656 pages. New York: John Wiley and Sons.

Irwin MT, Johnson SE and PC Wright. 2005. The state of lemur conversation in southeastern Madagascar: Population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. Oryx 39: 204-218.

Irwin MT, and JL Raharison (in prep.). Ecosystem in decay: Factors influencing primate species extinctions in forest fragments of Tsinjoarivo, Madagascar.

Irwin MT, Samonds, KE, Raharison JL, and PC Wright. 2004. Lemur latrines: Observations of latrine behavior in wild primates and possible ecological significance. Journal of Mammalogy 85: 420-427.

Irwin MT. 2006. Ecological Impacts of Forest Fragmentation on Diademed Sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar: Implications for Conservation in Fragmented Landscapes. Unpublished Dissertation, Stony Brook University.

Irwin MT. 2007. Living in forest fragments reduces Group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar, by reducing food patch size. American Journal of Primatology 69: 434-447.

Irwin MT. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: Higher density but lower viability in fragments? Biotropica 40: 231-240.

Isbell LA, and TP Young. 1993. Social and ecological influences on activity budgets of vervet monkeys, and their implications for Group living. Behavioral Ecology and Sociobiology 32: 377-385.

Isbell LA, Cheney DL, and RM Seyfarth. 1990. Costs and benefits of home range shifts among vervet monkeys in Amboseli National Park, Kenya. Behavioral Ecology and Sociobiology 27: 351-358.

Isbell LA. 1994. Predation on primates: Ecological patterns and evolutionary consequences. Evolutionary Anthropology 3: 61-71.

Iwamoto T, and RIM Dunbar. 1983. Thermoregulation habitat quality and the behavioral ecology of baboons. Journal of Animal Ecology 52: 357-366.

Janson CH, and ML Goldsmith. 1995. Predicting Group size in primates: Foraging costs and predation risks. Behavioral Ecology 6: 326-336.

Janzen DH. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2: 465-492.

Janzen DH. 1983. No park is an island: Increase in interference from outside as park size decreases. Oikos 41: 402-410.

Johns AD, and JP Skorupa. 1987. Responses of rain forest primates to habitat disturbance: a review. International Journal of Primatology.

Johns AD. 1986. Effects of selective logging on the behavioral ecology of west Malaysian primates. Ecology 67: 684-694.

Johns AD. 1987. The use of primary and selectively logged rainforest by Malaysian hornbills and implications for their conservation. Biological Conservation 40: 179-190.

Johns AD. 1988. Effects of selective timber extraction on rainforest structure and composition and some consequences for frugivores and folivores. Biotropica 20: 31-37.

Johns AD. 1991. Forest disturbance and Amazonian primates. In: HO Box (ed.) Primate responses to environmental change. London: Chapman and Hall. Pp. 115-135.

Johns AD. 1992. Vertebrate responses to selective logging: Implications for the design of logging systems. Philosophical Transactions of the Royal Society, London 335: 437-442.

Johnson AE, Knott CD, Pamungkas B, Pasaribu M, and AJ Marshall. 2005. A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. Biological Conservation 121: 495-507.

Jolly A, and RE Pride. 1999. Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: A33-year perspective. International Journal of Primatology 20: 359-371.

Jolly A, Dobson A, Rasamimanana HM, Walker J, O'Connor S, Solberg M, and V Perel. 2002. Demography of *Lemur catta* at Beretny Reserve, Madagascar: Effects of troop size, habitat and rainfall. International Journal of Primatology. 23: 327-354.

Jolly A, Koyama N, Rasamimanana H, Crowley H, and G Williams. 2006. Berenty Reserve: A research site in southern Madagascar. 2006. In: Jolly A, Sussman RW, Koyama N, and Rasamimanana H (eds.). New York: Springer. Pp. 313-331.

Jolly A, Rasamimanana HR, Kinnaird MF, O'Brien TG, Crowley HM, Harcourt CS, Gardner S, Davidson J. 1993. Territoriality in *Lemur catta* Groups during the birth season at Berenty, Madagascar. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 85–109.

Jolly A. 1966. Lemur Behavior: A Madagascar Study Guide. University of Chicago Press, Chicago.

Jolly A. 1984. The puzzle of female feeding priority. In Small, M. (ed.): Female Primates: Studies by Women Primatologists. New York, Alan R. Liss, pp. 197-215.

Jolly A. 1972. Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatologica 7: 335– 362.

Jolly A. 2003. *Lemur catta*, ring-tailed lemur, Maky. In: Goodman SM, and JP Benstead, eds. The Natural History of Madagascar. University of Chicago Press, Chicago. Pp. 1329-1331.

Jones KC. 1983. Inter-troop transfer of *Lemur catta* at Berenty, Madagascar. Folia Primatologica 40: 145–160.

Jules ES, and P Shahani. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. Journal of Vegetation Science 14: 459-464.

Junge RE, and ML Sauther. 2006. Overview on the Health and Disease Ecology of Wild Lemurs: Conservation Implications. In Lemurs: Ecology and Adaptation. Gould L and Sauther, ML (editors). Springer, pp. 423-440.

Kaplin BA. 2001. Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. International Journal of Primatology 22: 521-548.

Kapos V, Wandelli E, Camargo JL, and G Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: WF Laurance and RO Bierregaard Jr. (eds.): Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Chicago: University of Chicago Press 33-44.

Kapos V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5: 173-185.

Kappeler PM. 1990. Female Dominance in *Lemur catta*: More than Just Female Feeding Priority? Folia Primatological 55: 92-95.

Kappeler PM. 1998. To whom it may concern: The transmission and function of chemical signals in *Lemur catta*. Behavioral Ecology and Sociobiology 42: 411-421.

Kawecki TJ. 1995. Demography of source-sink populations and the evolution of ecological niches. Evolutionary Ecology 9:38–44.

Koyama N, Rasamimanana H, and RW Sussman (eds.). Ring-tailed Lemur Biology. New York, Sponger, pp. 32-42.

Koyama N, Soma T, Ichino A, and Y Takahata. 2006. Home ranges of ring-tailed lemur troops and the density of large trees at Berenty Reserve, Madagascar. In: Ringtailed Lemur Biology. Jolly A, Koyama N, Rasamimanana H, and RW Sussman, eds. New York Springer. Pp. 86-101.

Krauss J, Steffan-Dewenter I, and Tscharntke T. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological Conservation 120: 355-361.

La Fleur M, and L Gould. 2009. Feeding outside the froest: The Importance of Crop Raiding and an Invasive Weed in the Diet of Gallery Forest Ring-Tailed Lemurs (*Lemur catta*) following a Cyclone at the Beza Mahafaly Special Reserve, Madagascar. Folia Primatologica 80: 233-246.

Lande R. 1988. Anthropogenic, ecological and genetic foactors in extinction and conservation. Research in Population Ecology 40: 259-269.

Larson MA, Thompson III FR, Millspaugh JJ, Dijak WD, and SF Shifley. 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. Ecological Modelling 180: 103-118.

Laurance WF, and RO Bierregaard . 1997. Tropical Rainforest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Laurance WF, Bierregaard RO, editors. University of Chicago Press, Chicago.

Laurance WF, and MA Cochrane. 2001. Synergistic effects in fragmented landscapes. Conservation Biology: 1488-1535.

Laurance WF, and TJ Curran. 2008. Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. Australian Ecology 33: 399-408.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, and TE Lovejoy. 2000. Rainforest fragmentation kills big trees. Nature 404: 836.

Laurance WF, Ferreira LV, Rankin-de Merona J, and SG Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79: 2032-2040.

Laurance WF, Laurance SG, Ferreira LV, Rankin-de-Merona JM, Gascon C, and TE Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. Science 278: 1117-1118.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard Jr. OO, Laurance SG and E Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conservation Biology 16: 605-618.

Laurance WF, Lovejoy TE, and HL Vasconcelos. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16: 605-618.

Laurance WF. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy 71: 641-653.

Laurance WF. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79-89.

Laurance WF. 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation 69: 23-32.

Laurance WF. 1997. Hyper-disturbed Parks: Edge effects and the ecology of isolated rainforest Reserves in tropical Australia. In WF Laurance and RO Bierregaard Jr. (eds.): Tropical Forest Remnants: Ecology, Mangaement, and Conservation of Fragmented Communities. Chicago: University of Chicago Press pp. 71-83.

Laurance WF. 2002. Hyperdynamism in fragmented habitats. Journal of Vegetation Science 13: 595-602.

Lawes MJ, Mealin PE, and SE Piper. 2000. Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. Conservation Biology 14: 1088-1098.

Lawes MJ. 1992. Estimates of population density and correlates of the status of the samango monkey *Cercopithecus mitis* in Natal, South Africa. Biological Conservation 60: 197-210.

Levins R. 1969. Some demographic and genetic consequesnces of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Levins R. 1970. Extinction. pp. 77–107. In: Gesternhaber M. Some Mathematical Problems in Biology. American Mathematical Society, Providence, Rhode Island.

Lindenmayer DB, and JF Franklin. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Seattle, Washington: Island Press.

Lomolino MV. 1986. Mammalian community structure on islands: The importance of immigration, extinction, and interactive effects. Biological Journal of the Linnean Society 28: 1-21.

Loudon JE. 2009. The Parasite Eology and Socioecology of Ring-Tailed Lemurs (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) inhabitaing the Beza Mahafaly Special Reserve. Ph.D. University of Colorado at Boulder.

Lovejoy TE, Bierreguaard RO, Rylands AB, Malcolm JR, Quintela CE, harper LH, Brown KS, Powell AH, Powell GVN, Schubart HOR, and MB Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. In: ME Soulé (ed.), Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.

Lugo AE. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Australian Ecology 33:368-398.

MacArthur RH, and EO Wilson. 1963. An Equilibrium Theory of Insular Zoography. Evolution 14: 373-387.

MacArthur RH, and EO Wilson. 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press.

MacPhee RDE, and PA Marx. 1997. The 40,000 year plague. In: Goodman SM and Patterson BD, editors. Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, DC. p. 169-217.

Margules CR, and JL Stein. 1989. Patterns and distributions of species and the selection of nature Reserves: an example from Eucalyptus forests in south-eastern New South Wales. Biological Conservation 50: 219-238.

Margules, C. R. 1987. Single Large or Several Small Reserves? Nature Conservation: the Role of Remnants of Native Vegetation. In: Saunders DA, Arnold GW, Burbidge AA, and Hopkins JM. Surrey Beatty and Sons, Australia.

Marsh C. 1981. Ranging behavior and its relation to diet selection in Tana River red colobus (Colobus badius rufomitratus. Journal of Zoology 195: 473-492.

Marsh CW. 1981. Diet choice among red colobus on the Tana river, Kenya. Folia Primatologica 8: 157-191.

Marsh LK. 2003. The nature of fragmentation. In: LK Marsh (ed.) Primates in fragments: Ecology and conservation. Kluwer Academic: New York.

Mascie-Taylor C, and Bogin B. 1995. Human variability and plasticity. Cambridge: Cambridge University Press

May RM. 1975. Island biogeography and the design of wildlife preserves. Nature 245: 177-178.

Mbora DNM, and DB Meikle. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus. Biological Conservation 118: 67-77.

McLennan JA, Potter MA, Robertson HA, Wake GC, Colbourne R, Dew L, Joyce L, McCann AJ, Miles J, Miller PJ, and J Reid. 1996. Role of Predation in the Decline of the Kiwi in New Zealand. New Zealand Journal of Ecology 20: 27-35.

Melnyk M, and N Bell. 1996. The direct-use values of tropical moist forest foods: The Huottuja Amerindians of Venezuela. Ambio 25: 468-472.

Mertl AS. 1975. Discrimination of indivudals by scent in a primate. Behavioral Biology 14: 505-509.

Mertl-Milhollen AS, Moret EL, Felantsoa D, Rasamimanana H, Blumenfeld-Jones KE, and Jolly A. 2003. Ring-tailed lemur home ranges correlate with food abundance and nutritional content at a time of environmental stress. International Journal of Primatology 24: 969-297.

Mertl-Milhollen AS, Rambeloarivony H. KaiserVA, Gray L, Dorn LT, Williams G, and Rasamimanana H. 2006. The influence of tamarind tree quality and quantity on *Lemur catta*

behavior. In: Ringtailed Lemur Biology. Jolly A, Koyama N, Rasamimanana H, and RW Sussman, eds. New York Springer. Pp. 102-118.

Mertl-Muilhollen AS. 1979. Olfactory demarcation of territorial boundaries by a primate: *Propithecus verreauxi*. Folia Primatologica 32: 35-42.

Mertl-Muilhollen AS. 2000. Tradition in *Lemur catta* at Berenty Reserve, Madagascar. International Journal of Primatology 21: 287-297.

Mesquita RCG, Delamonica P, and WF Laurance. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biological Conservation 91: 129-134.

Miller DS, Sauther ML, Hunter-Ishikawa M, Fish K, Culbertson H, Cuozzo FP, Campbell TW, Andres GA, Chavey PS, Nachreiner R, Rumbiha W, Stacewicz-Sapuntzakis M, Lappin MR. 2007. Biomedical Evaluation of Free-Ranging Ring-Tailed Lemurs (*Lemur catta*) in Three Habitats at the Beza Mahafaly Special Reserve, Madagascar. Journal of Zoo and Wildlife Medicine 38: 201-216.

Millette JB, Sauther ML, and FP Cuozzo. 2009. Behavioral REsponsses to Tooth Loss in Wild Ring-Tailed Lemurs (Lemur catta) at the Beza Mahafaly Special Reserve, Madagascar. American Journal of Physial Anthropology 140: 120-134.

Milton K. 1980. The Foraging Strategy of Howler Monkeys: A study in primate economics. New York: Columbia University Press.

Muoria PK, Karere GM, Moinde NN, and MA Suleman. 2003. Primate census and habitat evaluation in the TAna delta region, Kenya. African Journal of Ecology 41: 157-163.

Murcia C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends in Ecology and Evolution 10: 58-62.

Mutschler T. 2002. Alaotran gentle lemur: Some aspects of its behavioral ecology. Evolutionary Anthropology 11(Suppl 1): 101-104.

Nakamichi M, and N Koyama. 1997. Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. International Journal of Primatology 18: 73-93.

Naughton-Treves L, Treves A, Chapman C, and R Wrangham. 1998. Temporal patterns of crop-raiding by primates: Linking food availability in croplands and adjacent forest. Journal of Applied Ecology 35: 596-606.

Naughton-Treves L. 1996. Uneasy neighbors: wildlife and framers around Kibale National Park, Uganda. PhD dissertation, University of Florida, Gainesville, FL.

Nee S, May RM, and MP Hassell. 1997. Two-species metapopulatin models. In: IA Hanski and ME Gipin (eds.): Metapopulation Biology. New York: Academic Press. Pp. 123-147

Njiforti HL. 1996. Preferences and present demand for bushmeat in north Cameroon: some implications for wildlife conservation. Environmental Conservation 22: 149-155.

Noss RF, and AY Cooperider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Washington, DC.

Noss RF, and B Csuti. 1997. Habitat fragmentation. In: Meffe GK, and CR Carroll (eds.) Principles of Conservation Biology. Sinauer Associates, Sunderland.

Nunn CL, and Altizer S. 2006. Infectious Diseases in Primates. Oxford University Press, New York.

O'Connor S. 1987. Human impact and primates in Madagascar. PhD dissertation. Oxford University.

Oates JF. 1977. The gueraza and its food. In: TH cutton-Brock-Brock (ed.): Primate Ecology. New York: Academic Press, pp. 275-321.

Oates JF. 1999. Myth and Reality in the Rain Forest. University of California Press, Los Angeles.

Olupot W. 2000. Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. Conservation Biology 14: 833- 843.

Onderdonk DA, and CA Chapman. 2000. Coping with forest fragmentation: The primates of Kibale National Park, Uganda. International Journal of Primatology 21: 587-611.

Palo M. 1994. Population and deforestation. In: K Brown and DW Pearce (eds.) The causes of tropical deforestation. London: UCL Press. Pp. 42-56.

Parga JA. 2006. Male Mate Choice in *Lemur catta*. International Journal of Primatology 27: 25-37.

Patel ER. 2005. Silky sifaka predation (*Propithecus candidus*) by a fosa (*Cryptoprocta ferox*). Lemur News 10: 25-27.

Patterson BD, and Atmar W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society 28: 65-82.

Patterson BD. 1987. The principle of nested subsets and its implications for biological conservation. Conservation Biology1: 323-334.

Pavelka MSM and AM Behie. 2005. The effect of hurricane Iris on food supply on black howlers (*Alouatta pigra*) in southern Belize. *Biotropica* 37: 102-108.

Pavelka MSM, McGoogan KC, and TS Steffens. 2003. Population size and characteristics of *Alouatta pigra* before and after a major hurricane. International Journal of Primatology 28: 919-929.

Pereira ME, Strohecker RA, Cavigelli SA, Hughes CL, and DD Pearson. 1999. Metabolic strategy and social behavior in Lemuridae. In: New Directions in Lemur Studies. Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, and Goodman SM, eds. New York, Kluwer Academic/Plenum. Pp. 93-118.

Peres CA, and J. Terborgh. 1995. Amazonian nature Reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. Conservation Biology 9: 34-46.

Peres CA, and MGM van Roosmalen. 1996. Avian dispersal of mimetic seeds in *Ormosia lignivalvis*: deceit or mutualism. Oikos 75: 249-258.

Peres CA. 2000a. Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. Conservation Biology 14: 240-253.

Peres CA. 2000b. Identifying keystone plant resources in tropical forests. Journal of Tropical Ecology 16: 287-317.

Peres CA. 2000c. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. Pp. 83-115. In: Hunting for Sustainability in Tropical Forests. J.G. Robinson & E.L. Bennett, eds. Columbia University Press, New York.

Peres CA. 2000d. Intergroup spacing and the ecology of group movements in Neotropical primates. Pp. 198-230. In: On the Move: How and Why Animals Move in Groups. S. Boinski & P.A. Garber, eds. University of Chicago Press, Chicago.

Perry JN, Liebhold AM., Rosenberg MS, Dungan J, Miriti M, Jakomulska A, and Citron-Pousty S. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. Ecography 25: 578-600.

Petter JJ, Albignac R, and Rumpler Y. 1977. Faune de Madagascar 44: mammiferes Lemuriens (Primates Prosimiens). Paris: ORSTROM/CNRS.

Pimm SL, Jones HL, and J Diamond. 1988. On the risk of extinction American Naturalist 132: 757-785.

Pope TR. 1990. The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behavioral Ecology and Sociobiology 27: 439-446.

Powzyk JA. 1997. The socioecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strageies and their possible repersuccsion on species-specific behaviors. PhD, Duke University , Durham, North Carolina.

Pulliam R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Raharivololona BM, and V Ranaivosoa. 2000. Suivi ecologique des lemuriens diurnes dans le Parc National d'Andohahela. Lemur News 5: 8-11.Rainforest Mammals. Conservation Biology 14: 1574-1579.

Rakotoarisoa SV. 2000. Contribution to the study of *Lemur catta* adaptation to mountainous zones of the Integral Natural Reserve of Andringitra. Lemur News 5: 50.

Ralainasolo FB, Ratsimbazafy JH, and NI Stevens. 2008. Behavior and diet of the Critically Endangered *Eulemur cinereiceps* in Manombo forest, southeast Madagascar. Madagascar Conservation and Development 3: 38-43.

Ralls K. 1971. Mammalian scent marking. Science 171: 443-449.

Ramos G, and B Ayala-Orozco. 2003. Population size and habitat use of spider monkeys at Punta Laguna, Mexico. In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 191- 208.

Rao M, and CP van Schaik. 1997. The behavioral ecology of Sumatran orangutans in logged and unlogged forest. Tropical Biodiversity 4: 173-185.

Rasamimanana HR, and E Rafidinarivo. 1993. Feeding behavior of *Lemur catta* females in relation to their physiological state. In: Lemur Social Systems and Their Ecologcial Basis Kappeler PM, and JU Ganzhorn, eds. New York, Plenum Press. Pp. 123-133.

Ratsimbazafy JH. 2006. Diet composition, foraging and feeding behvior in relation to habitat disturbance: implications for the adaptability of ruffed lemurs (*Varecia variegata editorium*) in Manombo forest, Madagascar. In Lemurs: Ecology and adaptation (Gould L, Sauther ML. (eds.). pp 403-422. New York, Springer.

Ratsirarson J, Randrianarisoa J. Ellis E, Emaday HJ, Efitroarany Ranaivonasy J, Razanajaonarivalonga EH, and AF Richard. 2001. Beza Mahafaly: ecologie et realites socio-economiques. Recherches pour Le Developpement, Serie Sciences Biologiques, No 18, Antananarivo, Madagascar.

Ratsirarson J. 2003. Beza Mahafaly Special Reserve, In: The Natural History of Madagascar. Goodman SM and JP Benstead, eds. University of Chicago Press, Chicago. Pp. 1520-1525.

Ratsirarson J. Randrianarisoa J, Ellis E, Emady JH, Efitroarany, Ranaivonasy J, Razanajaonarivalona EH, and AF Richard. 2001. Béza Mahafaly: écologie et réalités socio-

économiques. Recherches Pour Le Developpement, Série Sciences Biologiques, N0 18, Antananarivo, Madagascar.

Ratsiseraina IR. 2007. Etude de recouvrement de population de *Varecia variegata rubra* et de *Eulemur fulvus* a la suite d'une perturbation cyclonique dans le Parc National de Masoala, Madagascar. Lemur News 12: 61.

Redford KH, and JG Robinson. 1987. The game of choice: Patterns of Indian and colonist hunting in the Neotropics. American Anthropologist 89: 650-657.

Redford KH. 1992. The empty forest. Bioscience 42: 412-422.

Reed JM and AP Dobson. 1993. Behavioral constraints and conservation biology: Conspecific attraction and recruitment. Trends in Ecology and evolution 8: 23-256.

Remis MJ. 1997. Ranging and Grouping patterns of a Western lowland gorilla group at Baihokou, Central Aftican Republic. American Journal of Primatology 43: 111-133.

Richard AF. 1978. Behavioral Variation: Case Study of a Malagasy Lemur. Cranbury, New Jersey, Associated University Presses.

Rickets TH. 2001. The matix matters: Effective isolation in fragmented landscapes. American Naturalist 158: 87-99.

Ries L, Fletcher Jr. RJ, Battin K, and TD Sisk. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology, Evolution and Systematics 35: 491-522.

Robinson J, and K Redford. 1991. Sustainable harvest of neotropical wildlife. Pages 415-429 in J. Robinson and K. Redford, editors. Neo-tropical wildlife use and conservation. University of Chicago, Chicago.

Robinson JG, and EL Bennett. 2000. Hunting for Sustainability in Tropical Forests. Columbia University Press, New York.

Robinson JG, and RE Bodmer. 1999. Towards wildlife management in tropical forests. Journal of Wildlife Management 63: 1-13.

Rodriguez-Luna E, Domínguez- Domínguez LE, Morales-Mávil JE, and M Martínez-Morales. 2003. Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island. In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 229-250.

Rodriguez-Vargas AR. 2003. Analysis of the Hypothetical Population Structure of the Squirrel Monkey (*Saimiri oerstedii*) in Panama. In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 53-62.

Rubenstein D. 1997. Behavioral ecology and conservation policy: On balancing science, applications, and advocacy. In: Behavioral Ecology & Conservation Biology. T. Caro, ed.. Oxford University Press. Pp. 527-553

Rudran R and E Fernandez-Duque 2003. Demographic Changes over Thirty Years in Red Howler Population in Venezuela. International Journal of Primatology: 24(5): 925-947.

Rylands AB and Keruoghlian A. 1988. Primate populations in continuous forest and forest fragments in central Amazonia. Acta Amazonica 18: 291-307.

Sakai AK, Allendorf FW, Holt JS, David M. Lodge, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG. 2001. The Populations Biology of Invasive Species. Annual Review of Ecology, Evolution, and Systematics 32: 324-332.

Saunders DA, Arnold GW, Burbidge AA, and AJM Hopkins. 1987. The role of remnants of native vegetation in nature conservation: future directions. In: Saunders DA, Arnold GW, Burbidge AA, and AJM Hopkins (eds.). Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons, Chipping Norton, Australia.

Saunders DA, Hobbs RJ, and CR Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5: 18-32.

Sauther M. 1998. Interplay of Phenology and Repsoduction in Ring-Tailed Lemurs: Implications for Ring-Tailed Lemur Conservation. Folia Primatologica 69: 309-320.

Sauther ML, and FP Cuozzo. 2009. The Impact of Fallback Foods on Wild Ring-Tailed Lemur Biology: A Comparison of Intact and Anthropogenically Disturbed Habitats. American Journal of Physical Anthropology.

Sauther ML, Fish KD, Cuozzo FP, Miller DL, Hunter-Ishikawa M, and H Culberton. 2006. Patterns of Health, Disease, and Behavior Among Wild *Lemur catta*. In: Jolly A, Sussman RW, Koyama N, and Rasamimanana H (eds.). New York: Springer. Pp. 313-331.

Sauther ML, Gould L, and RW Sussman. 1999. The socioecology of the ringtailed lemur: Thirty-five years of study. Evolutionary Anthropology 8: 120-132.

Sauther ML, Sussman RW and FP Cuozzo. 2002. Dental and General Health in a Population of Wild Ring-tailed Lemurs: A Life History Approach. American Journal of Physical Anthropology 117: 122-132.

Sauther ML. 1992. Effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.

Schilling A. 1979. Olfactory communication in primates. In GA Doyle and RD Martin (eds.): The Study of Prosimiant Behavior. New York: Academic Press, pp. 461-542.

Schlichting CD and M Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, Mass.

Schwarzkopf L, and AB Rylands. 1989. Primate species richness in relation to habitat structure in Amazonian rainforest fragments. Biological Conservation 48: 6-12.

Sechrest W, Brooks TM, da Fonseca GAB, Konstant WR, Mittermeier RA, Purvis A, Rylands AB, Gittleman JL. 2002. Hotspots and the conservation of evolutionary history. Proceeds of the National Academy of Sciences 99: 2067-2071.

Sechrest WW, and TM Brooks. 2002. Biodiversity – Threats. Encyclopedia of Life Sciences. Macmillan Publishers Ltd., Nature Publishing Group/www.els.net. Pp. 1-8.

Shafer CL. 1995. Values and shortcomings of small Reserves. Bioscience 45: 80-88.

Shaw RP. 1989. Rapid population growth and environmental degradation: ultimate versus proximate factors. Environmental Conservation 16: 199-208.

Siegel S, and NJ Castellan. 1988. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill, Inc.

Silver SC, and LK Marsh. 2003. Dietary flexibility, behavioral plasticity, and survival in fragments: Lessons from translocated howlers. In: LK Marsh (ed.) Primates in Fragments: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 251-265.

Silverman BW. 1986. Density Estimation for Statistics and Data Analysis. London: Chapman and Hall.

Simberloff DS, and LG Abele. 1976a. Island biogeography and conservation: strategy and limitations. Science 193: 1032.

Simberloff DS, and LG Abele. 1976b. Island biogeography theory and conservation practice. Science 191: 285-286.

Simberloff DS, and LG Abele. 1982. Refuge design and island biogeographic theory: effects of fragmentation. American Naturalist 120: 41-50.

Simmen B, Hladik A, and PL Ramasiarisoa. 2003. Food intake and dietary overlap native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. International Journal of Primatology 5: 949-968.

Simmen B, Sauther ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L, and A Hladik. 2006. Plant Species Fed on by Lemur catta in Gallery Forests of the Southern Domain

of Madagascar. In: Ring-tailed Lemur Biology: *Lemur catta* in Madagascar. Jolly A, Sussman RW, Koyama N, and Rasamimanana H, eds. University of Chicago Press , Chicago. Pp. 55-68.

Singh KP, and CP Kushwaha. 2005. Diversity of Flowering and Fruiting Phenology of Trees in a Tropical Deciduous Forest in India. Annals of Botany 97: 265-276.

Singh M, and S Venanthe. 1990. Iner-population differences in the time budgets of bonnet macaues (*Macaca radiata*). Primates 31: 589-596.

Singh M, Kumara HN, Ananda Kuman M, and AK Sharma. 2001. Behavioral responses of Lion Tailed Macaques to a changing habitat in a tropical rain forest garment in the Western Ghats, India. Folia Primatologica 72: 278-291.

Skole D, and C Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. Science 260: 1905-1910.

Skorupa J. 1986. Responses of rain forest primates to selective logging Kibale Forest, Uganda: a summary report. In: Benirschke K, editor. Primates, the road to self-sustaining populations. Springer Verlag. New York

Slatkin M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16:393–430.

Slobodkin LB. 1969. Toward a predictive theory of evolution. In: Lewontin R, editor. Population Biology and Evolution. Syracuse: Syracuse University Press.

Smith AP, Horning N, and D Moore. 1997. Regional biodiversity planning and lemur conservation with GIS in Western Madagascar. Conservation Biology 11: 498-512.

Smith AP. 1997. Deforestation, fragmentation, and reserve design in Western Madagascar. In: Laurance WF, Bierregaard RO, Jr, editors. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago. Pp. 415-441

Smith TB, Kark S, Schneider CJ, Wayne RK, and C Moritz. 2001. Biodiversity hotspots and beyond: the need for preserving environmental transitions. Trends in Ecology and Evolution 16: 431.

Soma T. 2004. Feeding ecology of Lemur catta at Berenty Reserve, Madagascar: Immigrant and endemic plant species. Folia Primatologica 75 (Suppl.): 158-159.

Soma T. 2006. Tradition and Novelty: *Lemur catta* Feeding Strategy on Introduced Tree Species at Berenty Reserve. In: Ring-tailed Lemur Biology: *Lemur catta* in Madagascar. Jolly A, Sussman RW, Koyama N, and Rasamimanana H, eds. University of Chicago Press, Chicago. Pp. 141-159.

Soulé ME and B Wilcox. 1980. Conservation Biology: An evolutionary-ecological approach. Massachusetts: Sinauer Associates.

Strier KB and JP Boubli. 2006. A history of long-term research and conservation of northern muriquis (*Brachyteles hypoxanthus)* at the Estacao biologica de Caratinga/Rppn-RMA. Primate Conservation. Volume 20: 210.

Struhsaker TT. 2008. Demographic Variability in Monkeys: Implications for Theory and Conservation. International Journal of Primatology 29: 19-34.

Sultan SE, and HG Spencer. 2002. Metapopulation Structure Favors Plasticity over Local Adaptation. The American Naturalist 160: 271-283.

Sultan SE. 1992. Phenotypic plasticity and the neo-Darwinian legacy. Evolutionary Trends in Plants 6: 61–71.

Sussman RW. 1972. An ecological study of two Madagascan primates: *Lemur fulvus rufus* (Aude-bert) and *Lemur catta* (Linnaeus). Unpublished Ph.D. thesis, Duke University, Durham.

Sussman RW. 1974. Ecological distinctions in sympatric species of Lemur. In: Martin, RD, Goyle GW, and AC Walker, eds. Prosimian biology University of Pittsburgh Press, Pittsburgh, pp. 75-108.

Sussman RW. 1977. Socialization, social structure, and ecology of two sympatric species of Lemur. In: Chevalier-Skolnikoff S, Poirier FE, editors. Primate bio-social development: biological, social, and ecological determinants. New York: Garland Publishing. p 515–528.

Sussman RW. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. American Journal of Physical Anthropology 84: 43-58.

Sussman RW. 1992. Male life histories and intergroup mobility among ring-tailed lemurs (*Lemur catta*) International Journal of Primatology 13: 395-413.

Sussman RW and A Rakotozafy. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26: 241-254.

Sussman RW, and PA Garber. 2004a. Rethinking sociality: cooperation and aggression among primates. In: Sussman RW, and Chapman A. (eds.), The Origin and Nature of Sociality. Aldine de Gruyter, New York. pp. 161–190.St. Louis.

Sussman RW, and PA Garber. 2004b. Cooperation and competition in primate social interactions. In Campbell C, Fuentes A, MacKinNon KC, Panger M, and SK Bearder, eds. New York: Oxford University Press. Pp 636-651.

Sussman RW, and J Ratsirarson. 2006. Beza Mahafaly Special Reserve: A Research Site in Southwestern Madagascar. In: Ringtailed Lemur Biology: *Lemur catta* in Madagascar. Jolly A,

Sussman RW, Koyama N, and H Rasamimanana. New York, Springer Publisher: 43-51.

Swart J and Lawes MJ. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. Ecological Modelling 93: 57-74.

Tauraund L, and B Simmen. 2002. A major increase in the population of brown lemurs on Mayotte since the decline reported in 1987. Oryx 36: 297-300.

Taylor L, and RW Sussman. 1985. A preliminary study of kinship and social organization in a semi free-ranging group of *Lemur catta*. International Journal of Primatology 6: 601-614.

Taylor L. 1986. Kinship, Dominance, and social Organization in a Semi Free-ranging Group of Ring-tailed Lemurs (*Lemur catta*). Ph.D dissertation Washington University.

Teichroeb JA, Saj TL, Paterson JD, and P Sicotte. 2003. Effect of Group size on activity budgets of *Colobus vellerosus* in Ghana. International Journal of Primatology 24: 743-758.

Templeton AR, and JF Georgiadis. 1996. A landscape approach to conservation genetics: Conserving evolutionary processes in the African bovidae. In: JC Avise and JL Hamrick (eds.) Conservation Genetics: Case Histories from Nature. New York: Chapman and Hall. Pp 398-430.

Terborgh J, and SJ Wright. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. Ecology 75: 1829-1833.

Thomas CD. 2000. Dispersal and extinction in fragmented landscapes. Proceedings, Royal Society of London, Series B 267: 139-145.

Thomas SC. 1991. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. Biotropica 23: 68-83.

Tilman D, May RM, Lehamn CL, and MA Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

Travis JMJ. 2003. Climate Change and Habitat Destruction: A deadly anthropogenic cocktail. Proceedings of the Royal Society of Londaon 270: 467– 473.

Tsuji Y, and S Takatsuki. 2008. Effects of a typhoon on foraging behavior and foraging success of *Macaca fuscata* on Kinkazan Island, Northern Japan. International Journal of Primatology 29: 1203-1217.

Turelli M. 1997. Environmental heterogeneity, maternal effects, and spatial patterns of genetic variation. Evolution 51: 93–94.

Tutin CEG, Ham RM, White LJ, and MJS Harrison. 1997. The primate community of the Lope Reserve, Gabon: diets responses to fruit scarcity and effects on biomass. American Journal of Primatology 6: 313-336.

Tutin CEG. 1999. Fragmented living; Behavioral ecology of primates in a forest fragment in the Lope Reserve, Gabon. Primates 40: 249-265.

Umapathy G, and A Kumar. 2000a. The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, South India. Prmates 41: 119-126.

Umapathy G, and A Kumar 2000b. The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. Biological Conservation 92: 311-319.

Umapathy G, and A Kumar. 2003. Impacts of forest fragmentation on lion-tailed macaques and Nilgiri langur in western Ghats, South India. In: LK Marsh (ed.) Primates in Fragements: Ecology and conservation. New York: Kluwer Academic Publishers. Pp. 163-189.

Underwood AJ. 1992. Ecological research and (and research into) environmental management. Ecological Applications 5: 232-247.

van Schaik CP, Terborgh JW, and SJ Wright . 1993. The phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. Annual Review of Ecology and Systematics 24: 353-377.

van Schaik CP, van Noordwijk MA, de Boer FR and I den Tonkelaar. 1983. The effects of Group size on time budgets and social behavior in wild long-tailed macaques (*Macaca fascicularis*). Behavioral Ecology and Sociobiology 13: 173-181.

Van Tienderen PH, and HP Koelewijn. 1994. Selection on reaction norms, genetic correlations and constraints. Genetical Research 64:115–125.

Van Tienderen PH. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. Evolution 45:1317–1331.

Wallis J, and DR Lee. 1999. Primate Conservation: The prevention of Disease Transmission. International Journal of Primatology 20: 803-826.

Walsh PD, Abernethy KA, Bermejo M, Beyersk R, De Wachter P, Akou ME, and B Huljbregis. 2003. Catastrophic ape decline in western equatorial Africa. Nature 422: 611-614.

Warre RD, and RH Crompton. 1997. A comparative study of the ranging behavior, activity rhythms and sociality of *Lepilemur edwardsi* and Avahi occidentalis at Ampijora, Madagascar. Journal of Zoology 243: 397-415.

Watt DP. 1988. Environmental influences on mountain gorilla time budgets. American Journal of Primatology 15: 195 – 211.

Weaver JL, Paquet PC, and LF Ruggiero. 1996. Resilience and conservation of large carnivores in the rocky mountains. Conservation Biology 10: 964-976.

White FJ, Overdorff DJ, Balko EA, and Wright PC. 1995. Distribution of ruffed lemurs (*Varecia variegata)* in Ranomafana National Park, Madagascar. Folia Primatologica 64: 124-131.

Whitelaw DC, and ML Sauther. 2003. A preliminary survey and GIS analysis of ring-tailed lemur habitat use in and around Beza Mahafaly Reserve, Madagascar. American Journal of Physical Anthropology. Supplement 36: 183.

Whitelaw DC, Sauther ML, FP Cuozzo, and JE Loudon. 2007. Understanding the Power of Proximate Mechanisms: Patterns of Ring-tailed Lemur infant survival at Beza Mahafaly Special Reserve. 2007. American Journal of Physical Anthropology Supplement 44: 248.

Whitelaw DC, Sauther ML, Loudon JE, Cuozzo F. 2005. Anthropogenic change in and around Beza Mahafaly Reserve: methodology and results. American Journal of Physical Anthropology. Supplement 40: 227.

Whitelaw DC, Sauther ML. 2002. A preliminary survey and study of the effects of habitat differences on ring-tailed lemurs (*Lemur catta*) in and around Beza Mahafaly Reserve, Madagascar. Caring for Primates. Abstracts of the XIXth Congress of the International Primatological Society. Beijing: Mammalogical Society of China. Pp 323-324.

Wieczkowski J. 2004. Ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*). American Journal of Primatology 63: 125-138.

Wilcove DS, McLellan CH, and AP Dobson. 1986. Habitat fragmentation in the temperate zone. In: ME Soulé (ed.) Conservation Biology: The science of scarcity and diversity. Massachusetts: Sinauer Associates. Pp 237-256.

Wilcox BA. 1980. Insular ecology and conservation. In: ME Soulé and B Wilcox, eds. Conservation Biology: An Evolutionary-Ecological Approach. Massachusetts: Sinauer Associates. Pp 95-118.

Wilkie DS, and JF Carpenter. 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. Biodiversity and Conservation 8: 927-955.

Wilkie DS, and JT Finn. 1988. A spatial model of land use and forest regeneration in the Ituri Forest of nothereastern Zaire. Ecological Modelling 41: 307-323.

Wilson DS, and J. Yoshimura. 1994. On the coexistence of specialists and generalists. American Naturalist 144: 692–707.

Wilson EO, and EO Willis. 1975. Applied biogeography. In: Cody ML, and Diamond JM (eds). Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts.

Wolff JO, Schauber EM, and WE Edge. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conservation Biology 11: 945-956.

Wolfheim, JH. 1983. Primates of the World: Distribution, Abundance, and Conservation. Seatlle, WA: University of Washington Press.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution home-range studies. Ecology 70: 164-168.

Wright PC. 1987. Diet and ranging patterns of *Propithecus diadema edwardsi* in Madagascar. American Journal of Physical Anthropology 72: 271.

Wright PC. 2006. Considering Climate Change Effects in Lemur Ecology and Conservation. In Lemurs: Ecology and adaptation. Gould L, Sauther ML. (eds.). Pp 385-401. New York, Springer.

Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. Yearbook of Physical Anthropology 43:31– 72.

Wright SJ. 1996. Phenological responses to seasonality in tropical plants. In: Tropical Forest Plant Ecophysiology. Mulkey SS, Chazdon RL, and Smith AP, eds. New York, Chapman and Hall: 440-460.

Yahner RH, and CG Mahan. 1997. Behavioral considerations in fragmented landscapes. Conservation Biology 11: 569-570.

Yamashita N. 2002. Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. International Journal of Primatology 23: 1025-1051.

Yongzu Z. Guogiang Q, Yonglei L, and C Southwick. 1989. Exinction of Rhesus Monkeys in Xinglung, North China. International Journal of Primatology 10: 375-381.

Youssouf IAJ, and E Rasoazanabary. 2008. Discovery of Macrotarsomys bastardi at Beza Mahafaly Special Reserve, southwest Madagascar with observations on the dynamics of small mammal interactions. Madagascar Conservation and Development 3: 31-37.

Youssouf JIA 2009. Impacts bioécologiques de la colonisation de Rattus rattus sur les micromammifères autochtones dans la Réserve Spéciale de Bezà Mahafaly au Sud-Ouest de Madagascar. Dissertation, University of Tulear, Madagascar.

Ziegler TE, Epple G, Snowdon CT, Porter TA, Belcher AM, and I Kuderling. 1993. Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. Animal Behavior 45: 313-322.

Zimmerman BL, and RO Bierragaard. 1986. Relevance of the equilibrium theory of island biogeography and species area relations to conservation with a case from Amazonia. Journal of Biogeography 13: 133-143.